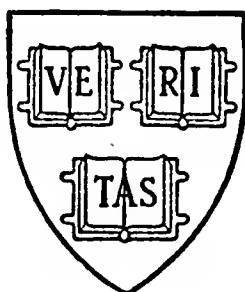


THE ROUGH-WINGED SWALLOW
A STUDY BASED ON ITS BREEDING
BIOLOGY IN MICHIGAN

WILLIAM A. LUNK

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Stelgidopteryx ruficollis (Vieillot)

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IN MICHIGAN**

PUBLICATIONS OF THE NUTTALL ORNITHOLOGICAL CLUB, NO. 4.

EDITOR, OSCAR M. ROOT

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by

WILLIAM A. LUNK

CAMBRIDGE, MASSACHUSETTS

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1962

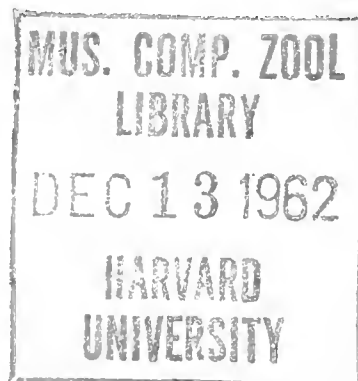
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WILLIAM A. LUNK

University of Michigan
Ann Arbor, Michigan
May 1, 1962

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INTRODUCTION

The swallows, family Hirundinidae, constitute a very distinct group of birds, having been referred to, for example (Witherby, *et al.*, 1940: 226), as "the best defined family of British Passeriformes." Their peculiar structure and habits have set them apart to such an extent, however, that their true relationship to other passerine families has never been satisfactorily established. Within the group, a baffling complex of minor morphological characters has made the recognition of interrelationships extremely difficult; and taxonomic treatment from the time of Sharpe and Wyatt's *Monograph of the Hirundinidae* (1885-94), and other early works, has undergone numerous fundamental changes. Mayr and Bond (1943) recommend the recognition of 21 genera, far fewer than the total number proposed by others. Peters (1960: 80-129) recognizes 20 genera. A minimal estimate of the number of species is about 75 (Mayr, 1946b: 67) or 76 (Peters, *loc. cit.*), many of these being polytypic, and many having acquired extensive synonymies. The nomenclature of swallows used in the present paper follows that of Peters (*loc. cit.*). Despite the fact that much work has been done in many parts of the world, adequate field data are available for relatively few of the forms; and the evaluation of these data has only begun. Extremely enlightening and stimulating is the discussion by Mayr and Bond, in which they attempt (p. 334) "to combine information from the two fields of morphology and field ornithology in order to arrive at a more natural classification." On the basis of form and coloration, egg color, nest type, and incubation habits, the swallows of the world are shown to fall into a number of rather clearly defined groups, some limited in distribution and some extremely widespread. The African and Neotropical Regions are by far the richest in number of species. Of North American swallows, almost half are clearly representative of types widespread in the Old World, while the rest belong to strictly New World genera. Among the latter is *Stelgidopteryx*, which is placed (Mayr and Bond, p. 341) in a group with generalized (and perhaps primitive) nesting habits, and clearly distinguished morphologically from all other genera.

The most important generic character is that the adults have the barbs of the outer web of the outer primary stiffened and free of barbules at the tip, and often recurved into minute hooklets, so as to produce (Ridgway, 1904: 56-57) "a file-like roughness when the finger is drawn along the edge of the quill from base toward tip." This

character is found also in the African Rough-winged Swallows of the genus *Psalidoprocne*; and this prompted Sharpe (1901: 202-203) to set up a separate subfamily, the *Psalidoprocninae*, separating the two genera from all other swallows. More recent authors, however, have uniformly doubted the existence of any close relationship between the two otherwise dissimilar "rough-winged" genera. Despite the frequently stressed superficial similarity between *Stelgidopteryx* and the Bank Swallows (*Riparia*), there is no indication of any close phylogenetic relationship. In fact, the present consensus seems to be that *Stelgidopteryx* is not closely related to any of the other genera, and that its nearest relatives may be such Neotropical forms as *Alopochelidon* and *Neochelidon*, particularly the former, which do not have the serrated outer primary (Mayr and Bond, *op. cit.*: 336, 340-341; Peters, 1960: 91-94).

At the present time only one species of *Stelgidopteryx*, the very widespread and variable *S. ruficollis*, is recognized. About ten accepted subspecies range from northern Argentina to approximately the northern border of the United States (Hellmayr, 1935: 38-48; Griscom, 1929; Brodkorb, 1942; Peters, *op. cit.*: 92-94). Within the limits of the United States, save for a small area in the extreme southwest, the only recognizable subspecies seems to be *Stelgidopteryx ruficollis serripennis*. This form is the principal subject of the present study; and to it I shall be referring hereafter, unless specifying otherwise.

In the north, the species (and subspecies) extends into Canada from the Puget Sound region and central British Columbia across to southwestern and southeastern Ontario, but reaches only central New York, central Vermont and New Hampshire, and extreme southern Maine. In the southwest, *S. r. serripennis* breeds to southern California and eastern Texas (where it intergrades with *S. r. psammochroa*); and there are no breeding Rough-wings below about the middle of the Florida peninsula.

The northern race is found in winter from southern California and southern Texas through most of Mexico, and south at least to Costa Rica and Panama. Stragglers are reported from southern Louisiana, southern Florida, and southeastern South Carolina (Wayne, 1895). The seasonal movements of the various subspecies are, however, complex (cf. Wagner, 1951; Cherrie, 1890: 335; Paynter, 1957; Skutch, 1960: 265), and have not been thoroughly worked out.

Frequent statements in faunal works and local lists refer to the observation, with increasing regularity, of Rough-wings in places where earlier studies found them rare or absent. Undoubtedly much of this apparent change is due to the increased number and skill of field observers. Nevertheless, ample evidence remains that some actual extension of range has been taking place in modern times. The possi-

bility of this has been given closest attention in relation to New England records (cf. Bagg and Eliot, 1937: 388-392). The species' distribution there was discussed by May (1930), who could already trace its changing status from that of a rare straggler in southwestern Connecticut (about 1900) to that of a fairly widespread breeding bird over the whole southern half of New England. More recently, the trend has continued (Griscom, 1940: 458; Griscom and Snyder, 1955: 165), and Maine records (Palmer, 1949: 367-368; Webb, 1950: 42) have appeared. Eaton (1914: 352-353) had "no doubt that the Rough-winged swallow has gradually extended its range" in New York during the preceding fifty years; Fleming and Lloyd (1920: 437) suggested "a general extension of range" in southern Ontario; Widmann (1911: 310), writing of Estes Park, Colorado, listed the Rough-wing as one of the species that seemed to be invading from the East, and referred to it as having "advanced through the foothills deeper into the mountains with the settlement of the valleys." Even in Michigan, Wood and Tinker (1910: 134) wrote of the Rough-wing as then "gaining a foothold" in Washtenaw County, although such accounts as that of Barrows (1912: 553) rather emphasize the failure of many to recognize the bird where it was present in the state.

Wood (1951: 288) records the Rough-winged Swallow in Michigan as a "summer resident north to Luce and Schoolcraft counties." Zimmerman and Van Tyne (1959: 36) call it a "fairly common summer resident north to the Straits of Mackinac." Manville (1949: 107) gives sight records from Marquette County; Zimmerman and Van Tyne mention, in addition, ones from Iron, Houghton, and Baraga counties. Throughout suitable parts of the Lower Peninsula it is a common bird. Even in the Douglas Lake area in Cheboygan County, Linsdale (1936: 161) found the Rough-wing's frequency of occurrence to be somewhat above the middle of his scale, among the birds recorded for the area. In the account of Wood (*op. cit.*: 288-290), the bird is reported as usually arriving, both in the Ann Arbor region and at Battle Creek, "in the third or fourth week of April," but in the northern part of the state apparently not until May. The scanty autumn records indicate that the species has for the most part left the state by the beginning of August, although there are a few records throughout August in the southern counties.

Brooks (1942: 12) has pointed out that "descriptions of bird behavior made at points away from centers of abundance and near the range limits of the species, are often misleading as regards the species as a whole; . . . observations made at these range extremities may, as time goes on, have a peculiar value in tracing the origin and evolution of new races." While southern Michigan is not so near the extreme fringe of the Rough-wing's range as to raise expectations

of any particular abnormalities, it approaches the northern extremity so far as the species as a whole is concerned. In this area, well populated with other species of Hirundinidae of various taxonomic and zoogeographical affinities, a study of the Rough-wing takes on special significance. As knowledge of its Neotropical representatives is accumulated, comparisons may bring to light behavioral adaptations that have accompanied the morphological ones, if the species spread and evolved, as has been postulated (Griscom, 1929: 68-69), from South America northward. Likewise, comparisons with more distantly related swallows will be of interest both directly and in relation to an ultimate understanding of the phylogeny of the family as a whole.

Part I
PRELIMINARY CONSIDERATIONS
FIELD STUDY

STUDY AREAS

Field work was carried on in southeastern Michigan, mostly in Washtenaw County, and the bulk of it in and around sand and gravel excavations east of Ann Arbor and southeast of the village of Dixboro (lat. 42.18°N., long. 83.40°W.), in Sections 18 and 19 of Superior Township (T.2S., R.7E.), where Rough-winged Swallows were nesting in considerable numbers. The sketch map, Figure 1, will serve to locate some of the main topographic features, and a number of the specific nest sites referred to. The large gravel pit designated as Pit "A", together with "D" and a number of nearby smaller excavations, is operated by the Whittaker and Gooding Company; Pits "B" and "C" were at the time of the field study being worked by Mr. Ray Schief. (The maps were actually drawn in 1951, and extensive changes have taken place in subsequent years. Pit "B" no longer exists.) Certain data were obtained in a small pit, owned by Mr. Campbell, west of Gale Road and southwest of Pit "A"; from scattered nests in Ann Arbor; at the large Killins Gravel Company pit on Liberty Road, just west of Ann Arbor; at Hell, Livingston County; near the Edwin S. George Reserve, Livingston County; and near Scio, Washtenaw County. At none of these other points, however, was any intensive work carried on.

TIME IN THE FIELD

The four nesting seasons of 1949 to 1952 were included in the study. During the latter part of the 1949 season (from early June, when the field work began), and during the major part of the nesting activity in 1950 and 1951, I visited the pits almost daily, and frequently twice a day. At other times observations were somewhat less frequent; and in 1952 I was seldom in the area more often than once a week. Individual periods of observation varied from an hour or two to all day. In general, I attempted to cover as much territory as was feasible at each visit, and so keep a maximum number of nests under observation.

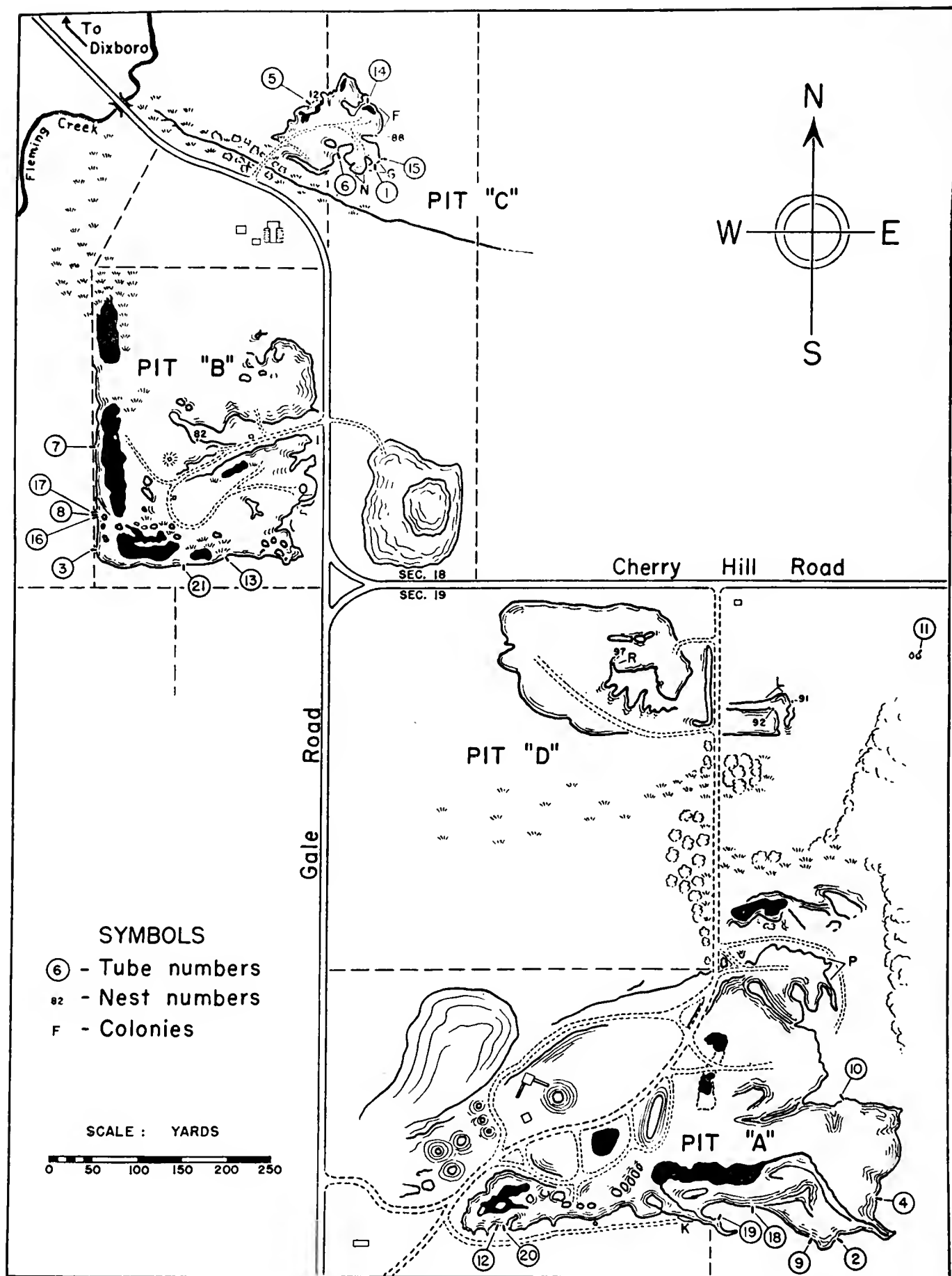
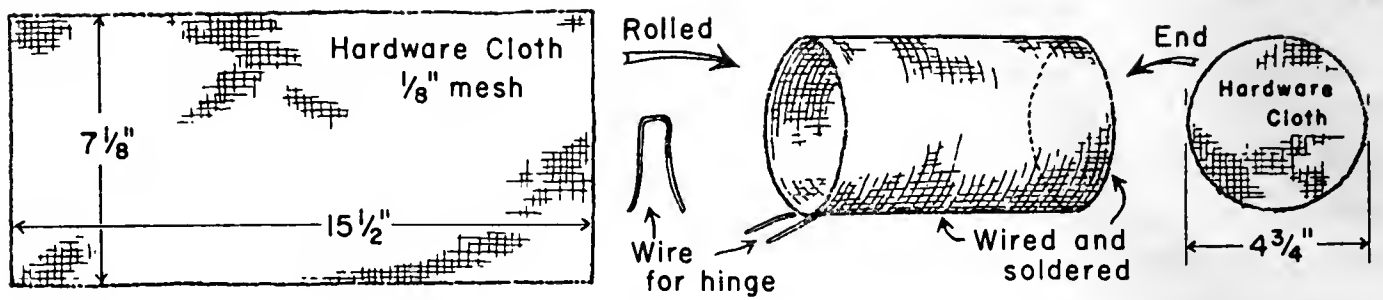


FIGURE 1. Sketch map of gravel pits (Superior Twp., Washtenaw Co., Mich.) constituting the principal study area, as they appeared in 1951. (Colonies indicated were principally of Bank Swallows.)

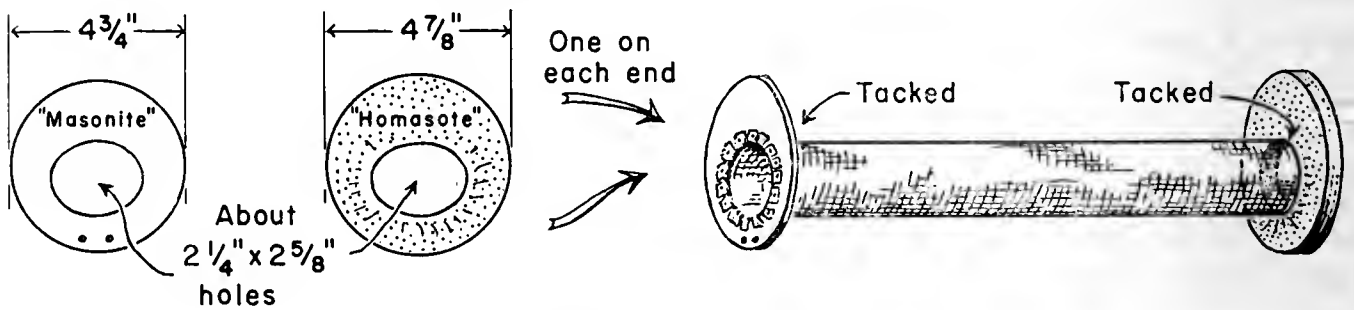
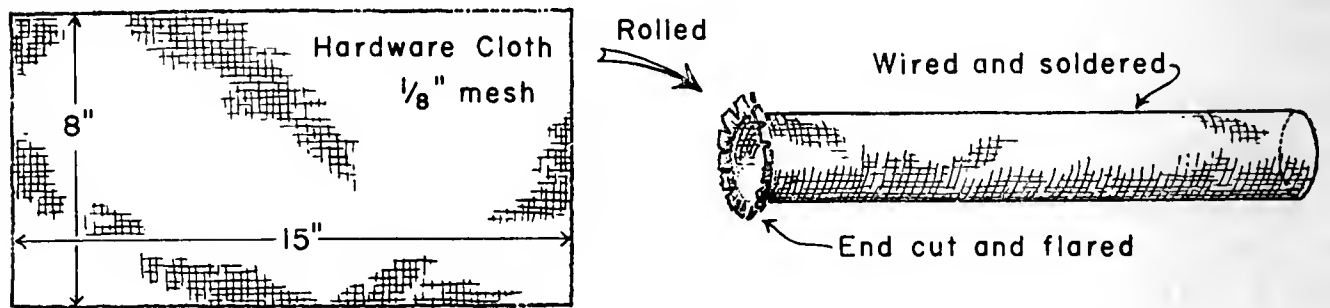
METHODS

Illuminated mirror. For investigating nests placed several feet back in narrow burrows, a simple device proved satisfactory. Using an ordinary two-cell flashlight as a handle and source of power, I attached as an extension about four feet of quarter-inch copper tubing, removing the lens and bulb of the flashlight and securing the tubing (soldered to a flanged metal base) by means of the retaining ring. I then threaded two insulated wires through the tubing, suitably soldered to terminals within the flashlight body at one end, and connected to a three-volt socket and bulb at the outer end, so that the original switch controlled the light. Also at the outer end of the tubing was mounted a small rectangular piece of mirror, about one inch high and two inches wide, bent downward at a 45-degree angle and protected above by a piece of light sheet metal. The bulb was fixed below and to one side of the tubing, just inside one edge of the mirror. With a little practice, this device can be worked carefully back into almost any burrow; and with the eye close beside the handle one can get a reasonably clear view of the nest by looking into the mirror. Lights and mirrors in various combinations are regularly used in the study of hole-nesting birds (cf. Stoner, 1936: 223; Skutch, 1945: 10); but I have never seen described in detail a method for introducing both the light and mirror far back into a cavity. Petersen's (1955: 238) "Ripariascope" was quite possibly similar to my implement.

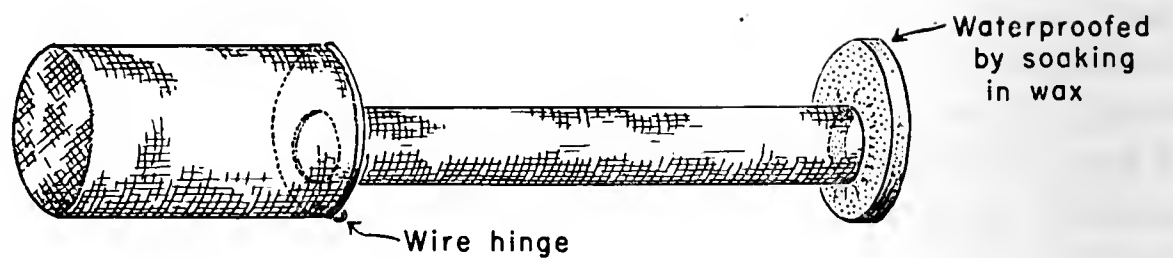
Artificial nest tubes. The apparatus just described allowed only the most cursory inspections of nest contents. For marking or careful examination of eggs or young, it becomes necessary to remove them entirely from the nest. Only an occasional Rough-wing nest is readily accessible for this; and inducing the birds to build in some sort of specially constructed container seemed a distinct possibility. The device I used consisted of two separate parts: a cylinder about five inches in diameter and two feet long, set into the face of a bank to provide a more or less permanent tunnel; and a loosely fitting liner, made of hardware cloth and composition boards, to contain the nest. While ordinary stovepipe served well enough as a casing, it tended to become crushed out of shape, and in time rusted badly. Entirely satisfactory was the heavy fiber duct, available in several sizes, which is used for the laying of underground wires and cables. The liners were constructed to be slid out and the front dropped on an improvised hinge; the nest is thus clearly visible and accessible, but remains virtually undisturbed. Figure 2 and Plate I show the construction and use of these nest tubes, which proved quite indispensable to my investigations. (See also illustration in Berger, 1961: 277.) Recently, an artificial nest, similar in function but quite different in design,



NEST CHAMBER



ENTRANCE TUBE



FINISHED LINER



CASING

FIGURE 2. Details of construction of an artificial nest tube for Rough-winged Swallows, as used during the present study.

has been used by Mayhew (1958: 11 ff.) for the study of Cliff Swallows (*Petrochelidon pyrrhonota*).

In 1950, 13 tubes were put in. Nests were begun in 13 (100 per cent), and completed in 11 (85 per cent), in that year. In 1951, 8 additional tubes were added. That year, nests were begun in 17 (81 per cent), and completed in 16 (76 per cent). In 1952, nests were begun and completed in 18 (86 per cent) of the tubes. During the three-year period, 19 of the 21 tubes (90 per cent) held at least one completed Rough-wing nest. Such high proportions of occupancy seem very remarkable, particularly since the containers were widely scattered, and in some cases placed deliberately in what seemed to me to be unlikely situations. The only bird that I have found usurping the nest tubes is the House Sparrow (*Passer domesticus*). I never knew Bank Swallows (*Riparia riparia*) to show any interest whatever; and I do not believe they would often accept any artificial site. They have been recorded as doing so, however (cf. Hellyar, 1927).

Miscellaneous techniques. Weighing was done in the field on an ordinary single-platform balance, fitted into a substantial wooden box with hinged cover, so that it could be leveled and partially protected from the wind. Measurements of adults and young, in the field, were taken with a celluloid millimeter scale. Eggs were most successfully handled by lifting them from the nest in a small plastic measuring spoon.

A few adults were captured by placing a small net over the entrance of the burrow. Blake (1953: 107), May (1930: 33), and Bergstrom (1953) report using such methods for the capture of Rough-wings, the former having also used a light to induce the bird to leave its hole. It appears particularly difficult to capture males; Gillespie (1934: 42-44) evidently succeeded in doing so repeatedly, but does not specify how the bird was "trapped." Most individuals I caught were females; and these were usually captured by hand as they remained on their nests while the tubes were opened.

In 1950 I took two nestlings and attempted to raise them by hand. The problem of feeding, however, proved very difficult, only live soft-bodied insects being fully satisfactory. The birds were never in a vigorous condition after such insects became difficult to obtain, and they shortly died. Chigi (1934: 4) reports the rearing of young European Swallows (*Hirundo r. rustica*) on a mixture of beef heart, cornmeal, and silkworm pupae. Richmond (1953) found only live insects suitable for young Purple Martins (*Progne subis*), and the young he raised were allowed to migrate with the other birds before cold weather set in.

Marking. For marking the individual eggs of a clutch I used purple indelible pencil; but I found it safer to carry also a small brush,

moisten it, and thus transfer the color from the pencil to the egg. During one season, thinking to avoid extra handling of the eggs, I simply placed dots of color on each. Each day, after a new egg had appeared, I placed one dot on each egg then in the nest, without lifting or turning them, the eggs thus receiving total dots in inverse proportion to their order of laying. This system proved satisfactory, but unnecessarily cumbersome. Thereafter I carefully removed whatever eggs were necessary, to see that each had a number placed upon it that indicated directly its position in the clutch.

For young Rough-wings too small to be fitted with regular aluminum bands, several methods of marking were tried. Most satisfactory by far were bits of colored thread, looped twice around the tarsus and tied loosely. I used a regular sequence of colors for the successive members of a brood. If adjusted initially to exactly the right size, the threads could be left until the nestlings were fledged; but usually I had to replace them once during the period of growth. Very seldom were any of these threads lost. Stoner (1945: 207) reports the use of this method for marking very young Cliff Swallows.

Banding was not a major aim of my study. However, I placed Fish and Wildlife Service bands on the young of a number of broods and banded adults whenever there was an opportunity. I banded 78 individuals in 1950 and 20 in 1951, making 98 in all.

While I made no attempt to mark large numbers of adults in the field, observations at certain nests were facilitated by the marking of the female. This was done by the process known to falconers as imping. Small white gull feathers trimmed down to a somewhat greater width than that of a Rough-wing rectrix, were dyed various bright colors, or left white. A fine steel wire was thrust up into the rachis of each, cemented in place, and left projecting. Capturing the bird to be marked, I clipped off one of the central rectrices about a third of the way from its base, and inserted a suitable marking feather into the end of the quill, securing it by means of a little acetate cement. This process was somewhat tedious, but provided a conspicuous mark, visible to the naked eye for distances of fifty yards or more, which did not in the least interfere with the bird's normal activities. Only light colors, such as yellow, orange, and white, were found suitable, however; and it was not possible for me to distinguish with certainty any pattern or combination, other than the mere flash of color against the otherwise dark tail. My few attempts to apply colored lacquers in such a way as to make them visible from a distance were unproductive, although Emlen (1952: 177-179) describes the very successful use of this method for his marking of Cliff Swallows.

NESTS STUDIED

In Table 1 are listed all of the Rough-wing nests from which I ob-

tained useful data, the 97 nests being arranged according to the numbers I arbitrarily assigned them in the field (gaps in the sequence

TABLE 1
SUMMARY OF ROUGH-WING NESTS, WITH THE STAGES COVERED BY MY OBSERVATIONS*

Nest No.	Location	Situation	Observations Covering							Remarks
			Building	Laying	Incubation	Hatching	Young in Nest	Leaving	Casual Only	
1949										
1	Ann Arbor	R.R. trestle	X	Female found dead
5	Scio	Bridge abutment	X	X	X
7	Hell	Burrow	..	X	X	Destroyed
8	George Res.	"	X	Feeding obs.
11	Pit "C"	"	..	X	X	X	X	X
12	" "	"	X	X	X
14	" "B"	"	X	X
17	" "	"	X	X
18	Campbell pit	"	X	..	X	...
1950										
19	Pit "C"	Tube 1	X	X	Destroyed
20	" "A"	" 2	X	X	X	X	X	X
21	" "B"	" 3	X	X	X	X	X	X
22	" "A"	" 4	X	X	X	X	X	X
23	" "C"	" 5	X	X	X	X	X	X
24	" "	" 6	X	X	X	X	X	X
25	" "B"	" 7	X	X	X	X	X	X
26a	" "	" 8	X	Deserted
26b	" "	" 8	X
27	" "A"	" 9	X	X	X	X	X	X
28	" "	" 10	X	X	X	X	X	X
29	Test pit	" 11	X	X	X	X	X	X
30	Pit "A"	" 12	X	Deserted
31	" "C"	Burrow	X	X	X	Destroyed
32	" "	"	X	X	X	X	X	X
33	" "B"	"	X	Deserted
34	" "	"	X	X	X	Destroyed
35	" "	"	X	X	X	"

* For explanation of certain localities and situations, see text and map (Figure 1).

TABLE 1 -- Continued

Nest No.	Location	Situation	Observations Covering							Remarks
			Building	Laying	Incubation	Hatching	Young in Nest	Leaving	Casual Only	
36	Pit "B"	Burrow	..	X	X	Destroyed
37	" "	"	X	Deserted
38	" "A"	"	..	X	X	X	X	Failed
39	" "	"	X	X	X	X	X	X
40	" "	"	..	X	Destroyed
41	" "	"	X	X	X	X	"
42	" "	"	X
43	Campbell pit	"	..	X	X	X	X
44	Ann Arbor	"	..	X	X	X	X	X
45	Pit "C"	"	X	X	X	X
46	" "	"	X	X	X	X	X
47	" "D"	"	X	X	X
59	Killins pit	"	X	..	X	Collected
60	" "	"	X	..	X	"
61	Pit "B"	Tube 13	X
1951										
62	Pit "C"	Tube 1	X	Deserted
63	" "A"	" 2	X	X	X	X	X	X
64	" "B"	" 3	X	X	X	X	X	X
65	" "A"	" 4	X	X	X	X	X	Destroyed
66	" "C"	" 5	X	Deserted
67	" "	" 6	X	"
68	" "B"	" 7	X	X	X	X	X	X
69	" "A"	" 10	..	X	Failed
70	" "	" "	..	X	X	X	X	X
71	Test pit	" 11	X	Deserted
72	Pit "A"	" 12	X	X	"
73a	" "C"	" 14	X	Female shot
73b	" "	" "	X	X	X	Destroyed
74	" "	" 15	X	X	X	Deserted
75	" "B"	" 16	X	X	X	X	X	X
76	" "A"	" 18	X	X	X	X	X	Destroyed

TABLE 1 -- Continued

Nest No.	Location	Situation	Observations Covering							Remarks
			Building	Laying	Incubation	Hatching	Young in Nest	Leaving	Casual Only	
77	Pit "A"	Tube 19	X	X	X	X	X	Destroyed
78	" "	" 20	X	Deserted
79	" "B"	" 21	X	X	X	X	X	X
80	" "C"	" 5	X	X	X	X	X	X
81	" "	Burrow	X
82	" "B"	"	X	X	X	X	X	X
83a	" "C"	"	X	Deserted
83b	" "	"	X	X	X	X
85	" "A"	"	X	X	Destroyed
86	Ann Arbor	"	X	X	X	"
87	Pit "A"	Tube 20	X	X	X	X	X	X
88	" "C"	Burrow	X	X	X	X	X	Destroyed
89	" "A"	"	X	"
90	" "	"	X	X	Deserted
91	" "D"	"	..	X	X	Destroyed
92	" "	"	X	X	X	X	X	X
93	" "C"	Tube 14	X	Deserted
94	Ann Arbor	Burrow	..	X	X	X	X	X
95	Pit "B"	"	X	X	X	X
97	" "D"	"	X	X
1952*										
98	Pit "C"	Tube 1	X	X	X	X	Destroyed
99	" "A"	" 2	..	X	X	X	X	X
100	" "B"	" 3	X	X	Destroyed
101	" "A"	" 4	X	X	X	X	"
102	" "C"	" 5	X	X	X	X	X	X
103	" "	" 6	X	X	X	X	X	X
104	" "B"	" 7	X	X	X	X	X	X
105	" "A"	" 9	X	X	X	X	X	X

* Observations were at wider intervals, and thus established events less definitely, than in previous years.

TABLE 1 -- Continued

Nest No.	Location	Situation	Observations Covering							Remarks
			Building	Laying	Incubation	Hatching	Young in Nest	Leaving	Casual Only	
106	Pit "A"	Tube 10	X	X	X	X	X	X
107a	Test pit	" 11	X	Deserted
107b	" "	" "	X	"
108	Pit "A"	" 12	X	X	X	X	X	X
109	" "C"	" 14	X	X	X	X	X	X
110	" "	" 15	X	X	X	X	X	X
111	" "B"	" 17	X	X	X	X	X	X
112	" "A"	" 18	X	X	X	X	X	X
113	" "	" 19	X	X	X	X	X	X
114	" "	" 20	X	X	X	X	X	X
115	" "B"	" 21	X	X	X	X	X	X

are due to the use of some numbers for Bank Swallow nests or for sites not actually occupied). The approximate extent of my observations at each nest is indicated.

GENERAL CHARACTERISTICS AND BEHAVIOR

Certain observed behavior patterns and other special considerations, not fitting logically into the following account of the nesting cycle, either have direct bearing upon my observations in the field, or are essential to a basic understanding of the Rough-wing as a subject for study.

APPEARANCE

The Rough-wing's dull coloration is matched by a comparatively (for a swallow) phlegmatic disposition. Although powerful on the wing, it spends considerable time quietly perching. After each more or less protracted flight, individuals or small groups are likely to sit for a while quietly looking about, preening, or sunning themselves. Koelz (1923: 39) described the Rough-wings at Ann Arbor, Michigan, as "more often taken than the other species of swallows on account of their habit of alighting in low bushes within easy gunshot." Certain favorite perches are frequently used as long as the birds remain in the breeding area.

Flight. As pointed out by Jones (1912: 177), the flight of the Rough-wing is more deliberate than that of the Bank Swallow, "more straight-away, with fewer abrupt turnings. The Rough-wing gives one the feeling of great reserves of energy." Blake (1948: 57-58) has a detailed description of the flight, and compares it with that of other North American swallows. Remarking that "the styles of flight . . . proved surprisingly diverse," he gives average figures ranging from about 2.8 to 3.9 wingbeats a second, as taken under various conditions. Blake concludes that a study of its flight only bears out the evidence from other sources that the Rough-wing is not closely related to any of our other swallows. The flight appears, at least, to be slower than that of the Bank (but Blake regards it as actually faster); its wingbeats often appear shallower, and when circling near the nest sites it tends to remain closer to the ground. Only in pursuit flights does it usually demonstrate the speed and maneuverability of which it is capable. Of particular interest is Miller's (1947: 370) description of the distinctly different flight of the shorter-winged *S. r. aequalis*, as compared to that of *S. r. serripennis*. He mentions as typical of the latter "the effect of long, trailing primaries."

In approaching a nest hole, Rough-wings ordinarily swoop low and enter on an upward slant, then appear to fold the wings slightly and dart directly through the opening (unless it is extremely small), without alighting until they are fairly inside. A common habit, if they are at all nervous or alarmed, is to make a number of diminishing circles, usually passing directly by the nest with each turn, before actually entering. Leaving the nest, the birds come straight out in a long glide, dropping sharply, with the wings held well back, and generally do not begin to flap until several feet from the entrance.

FEEDING HABITS

As would be expected from the behavior of the insects upon which they feed, I noted the Rough-wings (and swallows in general) feeding close to the ground in cool, cloudy, or windy weather. Even more than most swallows, the Rough-wings tend to feed over water, coursing back and forth close to the surface. Occasionally they appear to pick floating insects from the water itself. In general, I found them feeding at lesser altitudes than most swallows of other species, and apparently more adept at swooping between gravel piles, along narrow gullies, and over other irregular terrain.

The best summary of the food habits of the swallows is still that of Beal (1918), whose information on the Rough-wing (pp. 25-27) has been quoted by other authors, such as Howell (1924: 269), from whom Dingle (1942: 429) has quoted in turn. Insect food amounted to 99.23 per cent of the total. According to Beal's summary (p. 28),

the Rough-wing's diet, in no way strikingly different from that of other North American swallows, tends to be low in Coleoptera, Hemiptera, and Lepidoptera, and proportionately a little high in Diptera and Hymenoptera.

The specimens I collected carrying food for young had their mouths filled almost exclusively with Diptera; and the food items I have been able to see adults carrying have always been rather small, soft-bodied insects. My incidental observations support the statement of Beal that "lepidoptera are eaten sparingly by the rough-wing" (only a few moths and caterpillars are mentioned). On three occasions I observed flying butterflies, two of them *Pieris* sp. and one *Papilio polyxenes*, so close in front of Rough-wings (two perched, two flying, and three perched, respectively) that they could not possibly have failed to see them. Yet the swallows exhibited no interest in the passing insect.

VOICE

The Rough-winged Swallow is uniformly described as a generally silent bird. Its calls are subdued, and little varied. They are quite distinctive, however, once their peculiar quality has been fixed in mind. It would be useless to compile a list of all the syllabifications by which various writers have sought to describe these simple utterances. Such diverse spellings as "*tritrit*" (Saunders, 1951: 98-99); "*quiz-z-z-zeep; quiz-z-z-zeep*" (Dingle, 1942: 430, citing Dickey MS); "*dzip-dzip*" (Blake, 1947); "*zeetle-tzeet*" (Grinnell and Storer, 1924: 503); "*pssrt, pssrt*" (Grinnell, Dixon, and Linsdale, 1930: 290); and "*psud, psud, psud*" (Stone, 1937: 697) have been used. After many attempts to transcribe them, I settled upon something like "*brrrrt*" or "*brzzzt*" as most satisfactory, to my own ear; there being no actual vowel sound produced, so far as I can tell. The notes are nearly always separate and distinct, and successive ones similar; thus to my mind the term "twitter" is quite inappropriate, despite its use by Saunders (*loc. cit.*), Forbush (1929: 161), and others. Miller (1947: 370) has described *S. r. aequalis*, as observed by him in Colombia, as differing "appreciably from the races of Rough-winged Swallow of North America in quality of note, which is less guttural." Skutch (1960: 265), writing of the Rough-wing in Costa Rica, alludes to "soft, clear, singing notes" and "a brief, musical trill," evidently unlike anything uttered by the birds in the North.

Variations. Most of the notes of *S. r. serripennis* adults are variants of the same basic sound, considerably modified in pitch and inflection, and repeated in differing rhythms. This is in agreement with Saunders, who says further (1951: 98-99): "This note in one individual seems to be always on the same pitch, but individuals differ somewhat in

pitch.” This latter difference, I concluded, is largely a matter of sex.

The most distinctive call, that which I have thought of as the “territorial” note, is apparently uttered exclusively by the male. It is heard early in the spring, when the birds arrive and begin selecting sites, and throughout the nesting season, whenever a male is close to a site he regards as his own and other individuals are in the vicinity. The call is characterized by low pitch, short quick notes (three or four a second, estimated), each with a suggestion of rising inflection, and comparatively soft, liquid quality. In its simplest form, as when a perched male recognizes the passing of another Rough-wing at some distance, it consists only of a single very soft *brrrrt* or *brrrt-brrrt*. The call, however, may be extended into a whole series of rapid notes, being sometimes louder, with a quality of considerable excitement. At times it seems to function as the male’s alarm call.

Next most frequently heard are the alarm notes of the female, given in response to any disturbance at or near the nest. Sometimes these notes are single, and sometimes grouped, in a series of from two to six or eight, at somewhat irregular intervals. The individual notes vary in length, but are always much longer than those of the type last described, and slower (never over one or two a second); the pitch is noticeably higher, and the quality more grating: *brzzzzzt*, *brzzzt brzzzt brzzzt*, etc.; there is no upward inflection. These calls are evoked both by the presence of other Rough-wings in the vicinity, and by external disturbances. Very commonly, one or two single notes of this type are uttered by a female as if in response to the low quick note of a male. The male also has alarm notes of this sort, heard much less frequently, and I think always in response to some special disturbance. When both birds of a pair are circling and calling, however, the difference in pitch is usually quite evident, the male’s notes being much the lower, and less persistently reiterated.

During violent chases, one bird seems usually to be emitting a continuous series of rather high notes, uttered singly. I could not determine which bird was responsible, although the pitch and quality of the notes were most suggestive of those normal for the female. In the Bank Swallow, however, Petersen (1955: 242) found that only the male “sings” during “sexual chase.” Occasionally, I noted a special high, short, sharp note, uttered several times, during actual fighting. The sex of the individuals concerned was always in doubt; but it is most probable that they were males. Infrequently, I heard females utter single, soft, conversational notes, while around the nest; but generally speaking the females, when not alarmed, were silent.

The notes of the young, at the time of nest leaving, are still slightly falsetto, somewhat higher and weaker than those of the adults.

SEX DIFFERENTIATION

The sexes of the Rough-wing being, from a gross standpoint, alike, it becomes necessary to analyze such minor differences as do exist.

Plumage. Beyond, in discussing the serration of the outer primary, I point out the difference in its degree of development in the two sexes. This appears to be a fairly constant character, usable for determining the sex of birds in the hand: while the adult female may show considerable roughness due to the projecting and stiffened ends of the barbs, only the male ordinarily acquires distinctly recurved hooklets.

There are subtle but often useful differences in coloration. Even in the field, when comparison of two or more individuals is possible, it is sometimes very evident that the males average richer brown above, clearer gray and white below, darker-winged, and more contrastingly shaded about the face.

Grinnell and Storer (1924: 503) point out that "the under tail coverts of the males are broader and longer than those of the females." This is conspicuously true of fully adult specimens examined in the hand; and frequently serves as a supplementary character when living birds are under observation. There is a general tendency toward more luxuriant plumage in the male. The primaries and rectrices are somewhat broader than in the female; and even the contour feathers appear to be a little longer and broader. (A certain amount of this difference may be a result of greater wear affecting the plumage of the female, in the course of her nesting activities.) During a certain period, the presence of a brood patch in the female is diagnostic.

Size. Ridgway (1904: 59) gives measurements of series of Rough-wings (= *S. ruficollis* subsp.) from various areas in North and Central America, and in his table the average dimensions for females, particularly the wing lengths, are uniformly less than for males. I have made measurements of a series of 25 males and 20 females, all from Michigan, in the University of Michigan Museum of Zoology (occasionally abbreviated beyond as U.M.M.Z.) and in my own collection. Using only the wing length (the most convenient index) I find that males range from 107 to 114 mm. (averaging $109.82 \pm .038$ mm.) and females from 99 to 107 mm. (average, $103.33 \pm .044$). Thus females average about 5.9 per cent shorter winged than males; and in the series I examined there was practically no overlap. A hasty measurement of the wing of any bird captured in the field gives a reasonably good clue to its sex. Fourteen adult individuals handled at various times during my investigations, and judged from all indications to be females, had wing lengths ranging from 100 to 105.5 mm.; four supposed males caught ranged from 108 to 113 mm. in wing length. Frequently, the mere difference in size between the members of a pair is sufficient to distinguish them in the field.

As a matter of general interest, the wing lengths of two banded females I measured during two successive seasons are found to have remained rather constant. The wing of No. 50-11123 measured 104 mm. in 1951 (May 11) and 105 mm. in 1952 (June 14). Number 50-11129 had a wing measuring 105.5 mm. in 1951 (May 22) and 104 mm. (considerably worn) in 1952 (June 15). Neither showed any sign of immaturity when first taken.

Posture. In his paper on the Bank Swallow, Beyer (1938: 128) refers to one member of the pair he was observing as "more alert and masculine in appearance." While this statement is a trifle surprising, it nevertheless has real meaning. The male Rough-wing's whole bearing is one of watchful aggressiveness; it is reflected in an indefinable way in his movements and in the positions he assumes. Davis (1937: 69) has noted that the male Barn Swallow (*Hirundo rustica erythrogaster*) habitually raises the crown feathers, so as to give a ball-like shape to the head. In the case of the male Rough-wing, the effect is that of a more angular head, with a suggestion of a crest; the female's ordinarily appears lower-crowned and rounder. Both sexes at times raise the feathers of the crown, but the male appears to do so more regularly; furthermore, as I have already remarked, the feathers themselves — and this seems to me particularly true when the crown region of skins is examined — are somewhat longer and fuller in the male. As an example, I would call attention to the familiar photograph by Allen (1933: 122), which was also used later by Bent (1942: Pl. 62 lower); the individual pictured could, in my opinion, hardly be other than a male.

Summary. It is by a combination of criteria that I have been able to distinguish the sex of individuals in a fair number of situations; conversely, it is due to the lack of any one conspicuous and infallible character that I have on many occasions been forced to leave the matter of sex discrimination in doubt.

AGE DETERMINATION

It was of interest, whenever possible, to distinguish adults in their first breeding season. There seems to be considerable correlation with age in the degree of development of the serration of the first primary. I do not believe, however, that this is entirely dependable. I have seen birds I would otherwise judge to be only a year old which had relatively well-developed serrations; others, which appeared fully adult, had them rather weak. A most useful character seems to be the retention of a few pinkish juvenal feathers in the chin and upper throat, throughout the first winter and the following summer. Whether or not this is a universal irregularity

in the postjuvenal molt, certainly it is not exceptional, as examination of a number of specimens in the field, or of any good series of skins, will show. Ridgway (1904: 58) remarked upon this as "possibly a remnant of the immature plumage." Such evidence as I have obtained, from captive or banded individuals and from comparisons in general, points to the correctness of this assumption.

BEHAVIOR AT THE NEST

I collected many data on the behavior of adults present when I examined the contents of nests. Before building has begun, any close approach to the site selected for the nest is likely to arouse an immediate response from the pair concerned. If they are in the vicinity at all, which they generally are, both circle close in evident excitement. During the early stages of building, this behavior continues; but as the nest nears completion the birds develop a surprising tendency to remain away from it for long periods, and to display little concern even if present. For a few days after the nest is completed, and during the laying of the first few eggs of the clutch, it is unusual to see or hear any sign that the nest is still occupied.

After the commencement of incubation, it is normal to flush the female from the nest as one approaches. She circles, calling constantly in evident distress, as long as the disturbance continues. The male is now more likely to be present also, and to show similar concern. As incubation progresses, the attachment of the pair to the nest site grows even stronger, until it is not uncommon to have the female remain on the eggs so persistently that she must almost be forcibly pushed off. The behavior of the adults remains essentially the same until the time for brooding is past. Then the parents are likely to spend more time far afield in their search for food. When present, however, they continue to show essentially the same solicitude until the young have left the nest.

This pattern of changing behavior is useful when nests are being located, as an aid in determining the stage of nesting.

Part II
PRELAYING STAGES
NESTING SITES

Mayr and Bond (1943: 339), in a key to the nidification of New World swallow genera, include *Stelgidopteryx* as building "in burrows in banks which had been excavated by other species . . . (also at times in the crevice of a bridge or building)"; under the heading "In self-excavated burrows in banks," again appears "*Stelgidopteryx* (occasionally)." In this country the habits of the mud-nest-building Barn and Cliff Swallows, the burrowing Bank Swallow, and the typical hole-nesting Tree Swallow (*Tachycineta bicolor*), Violet-green Swallow (*Tachycineta thalassina*), and Purple Martin, are so familiar as to require but passing mention. Likewise, the curiously varied habits of the Rough-wing are evidenced by numerous and widespread accounts.

VARIETY OF SITES

In attempting to classify the principal nesting sites recorded in the literature, along with those in my own notes, and in unpublished notes which others have made available to me, I arrived at some eleven arbitrary categories.

In the first, we may consider holes excavated in banks, whether by the birds themselves or by other species, and whether isolated or in colonies. In Michigan they are certainly the sites most commonly used, and 42 of the nests listed in the present study (see Table 1), plus others not designated, fall into this group.

Secondly must be considered natural rock crevices, or fissures in cut banks, railroad embankments, shale cliffs, and the like. These are often in strata not suited to digging, and are distinguished from the preceding by being of more or less fortuitous origin. Wherever such sites are available, they are regularly used. Taken together, situations under this heading and the preceding comprise by far the majority of those recorded, and are the most "natural" nesting sites of the Rough-wing over its range as a whole.

Sites of a third type are provided by the exposed ends of drain pipes. These have received special comment in a number of instances (cf. Case, 1905; Chapman, 1938; Dickey, 1919; Doolittle, 1919; Lewis,

1944; Shufeldt, 1913). Such sites are eminently suitable, and may in fact contribute to the persistence of Rough-wings in areas that would not otherwise offer nesting possibilities. During the summer of 1950, I saw adults entering and leaving one of the open drain pipes in the retaining wall along the Huron River, in the heart of Ypsilanti. Van Tyne (unpubl.) informed me that, for some years, similar situations have been regularly occupied along the Detroit River in Detroit, and at other points in Michigan.

Crevices in masonry might be considered in another category of man-made sites. This, like the preceding, includes situations that are enclosed except for a single means of access—this may often be extremely small, so that the adults can barely squeeze through, as in one nest upon which I made observations (Nest 5). Nestings in stonework are not uncommon, and were recorded, for example, by Burns (1924: 83) in Pennsylvania, Griscom (1933: 126) in New York, and Wayne (1918: 439) in South Carolina.

A great many suitable sites are found on ledges and in crannies, under bridges, abutments, culverts, wharves, and other structures, which are more exposed than those just mentioned, although always very heavily shaded. With these would be included my Nest 1, on a girder beneath a railroad trestle.

Somewhat less common, apparently, are nests located in and about buildings, but references to them are numerous. Nickell (1949) has described a very bulky nest on top of a tool cabinet in a garage, at Bloomfield Hills, Michigan. During several seasons, Larry Camburn has made observations (unpubl.) on the nesting of Rough-winged Swallows in a ventilator pipe of an outbuilding, and on ledges inside a barn, at the Edwin S. George Reserve, Pinckney, Michigan.

Eifrig (1919: 523) reported a pair of Rough-wings near Chicago that were nesting close to a pair of Tree Swallows in a hole in the top of a dead cottonwood. As far as I have been able to discover, this is unique among specifically recorded sites, though such authors as Forbush (1929: 161) and Dawson (1903: 282) include holes in trees in their lists of general nest sites.

It is not surprising to find the Rough-wing making use of suitable crevices in and around caves, in regions where these occur (cf. Hibbard, 1935; Brodkorb, 1942: 217; Griscom, 1932: 286). The reference of Pearse *et al.* (1938: 229) to “mud nests [constructed] on the roofs of caves” in Yucatan, however, is almost certainly the result of some error of observation or identification.

To the best of my knowledge, there are no previously published accounts of Rough-wings nesting in any sort of deliberately placed artificial container. Therefore, the 53 nests (Table 1) in nest tubes are worthy of a separate category. It often appeared that the containers were selected in preference to more usual sites.

Special mention should be made of Rough-wing nests aboard boats. The interesting but vague account by Hoxie (1901) of "The Rough-wings of the Hercules" tells of repeated attempts by a pair to nest in the hawse pipe of the tug by that name, working in the harbor of Port Royal, Virginia, and making the trip to Beaufort three times a week. After the *Hercules* left port, there was apparently an unsuccessful nesting attempt on the *Nantucket* as well. Howell (1924: 268-269) gives a similar account, quoted by Dingle (1942: 427), of "one or more pairs" nesting "on a buttress beneath the deck of a transfer steamboat which made daily trips on the Tennessee River from Guntersville to Hobbs Island, a distance of 24 miles," the birds following the boat to feed their young.

A final category could include sites not seeming to fit any of the preceding groups. One reported by Jedlicka (1937: 379, ed. note) was in a great cinder and slag dump near Cleveland. Described to me by Van Tyne (unpubl.) was one in an abandoned kingfisher's hole in a large sawdust pile, in Crawford County, Michigan.

BURROWS

In regard to the origin of the burrows in banks, so commonly occupied by nesting Rough-winged Swallows, an implied controversy exists. Statements in the literature range from one extreme to the other. Dingle (1942: 426) and Pearson *et al.* (1959: 249), for example, represent the birds as usually or always excavating their own burrows; Todd (1940: 369) and Allen (1933: 121) make flat statements that they cannot or do not dig. The truth, most probably, lies somewhere between.

Literature. When so much has been written about the Rough-wing's readiness to take over any abandoned hole of another species, we can hardly assume that nesting burrows are *usually* dug by the swallows themselves, although this has frequently been taken for granted (cf. Burns, 1924: 83; Ridgway, 1878: 164; Shufeldt, 1913; Dingle, *loc. cit.*). The Bank Swallow is preëminently a burrower. Birds of this species have hardly arrived in the spring before they begin to cluster about freshly cut banks and start sporadic digging; even the young recently out of the nest display a digging response (Stoner, 1936: 201). The Rough-wing shows no such obvious signs of instincts in that direction. The problem of discovering to what extent it *does* excavate involves first a search for really concrete accounts of observed instances. And when references have been critically sifted, there are left but a handful that seem to warrant special consideration. Burns (*loc. cit.*) stated that the Rough-wing "burrows in a similar fashion to that of the preceding species [Bank Swallow],

though it is perhaps more apt to use its feet in scratching out the dirt." Bailey discussed at some length (1913: 261-262) the requirements for digging and the characteristics of the burrows, which he said were "made by the birds using their feet to scratch with, and push the dirt backward out of the tunnel." Van Fleet (1876) stated that they, "on finding a decayed root of sufficient size, leading in from their favorite sand banks, remove the soft punky wood, following the winding of the root, until they have arrived at [sic] a suitable distance — about two feet — where, after enlarging the cavity, they place their nest." He also described their infrequent excavating as "done in a very slovenly manner," and said "invariably their holes have been much larger than is apparently necessary." None of these authors gave any indication as to how much actual observation was used in formulating their ideas. Among those who have implied that digging might have been observed are Huey (1928: 158), Dawson (1903: 282), Eliot (1932: 102), and Sutton and Pettingill (1942: 23), but just how specific such writers have meant to be is not clear. Finally, Weydemeyer (1933: 362), calling particular attention to the discrepancy in the records, states that in Montana "Rough-winged Swallows regularly excavate their own burrows," and makes the positive statement: "I have observed them digging burrows in banks of clay, of sand, and of gravel." He leaves the matter without elaborating upon the nature or extent of his observations; but upon inquiry he has reaffirmed his convictions and stated (letter) that he has watched "the progress of tunneling" on various occasions.

Observations. I have five series of field notes, three taken in 1950, and two in 1951, which record the kicking out of a few spurts of sand by individual Rough-wings investigating burrows. In no case was the burrow in question subsequently used for nesting (unless by Bank Swallows, which in every case were believed to have dug them). In no instance was any visible change made in the hole. These brief observations do prove that the Rough-wing, on occasion, goes through the motions of digging, and indicate that it might be physically capable of enlarging a hole already begun, or even of undertaking a complete excavation. They substantiate the statements that the work would be done principally by use of the feet.

Otherwise, however, my evidence is entirely negative. The activity just described was quite out of the ordinary, and of a most desultory character. It appears that during my studies no Rough-wing nest, of nearly a hundred built in the area, was in a hole excavated by the birds themselves. Without exception, burrows were known, or could be presumed, to be unused or abandoned holes of other species. At certain times and places suitable holes were evidently at a premium

—yet not even then did the Rough-wings exhibit the slightest tendency to do any burrowing for themselves. I have no evidence that they even deepened or enlarged any existing burrow before building.

It would be absurd, on the basis of localized studies, to state that the Rough-winged Swallow *never* does any serious excavating. From all indications, however, it does so rarely, if at all, in this region. Skutch (1960: 268) has “no knowledge of Rough-winged Swallows digging tunnels for themselves in Central America”; he repeatedly refers (*op. cit.*: 265-268) to their taking over unused burrows of other species. We are in great need of some full and objective accounts from other areas, where the habits of the birds may be very different.

It is noteworthy that a certain amount of similar disagreement is apparent in accounts of the African Rough-wings, Moreau (1940: 235) having concluded in regard to *Psolidoprocne holomelaena massaica*: “I have no evidence that they ever do any excavation.”

COLONIALISM

Observers have nearly unanimously reported the Rough-wing as far less colonial in habits than the Bank Swallow. It is found most often in isolated pairs, scattered groups, or small colonies. Wood (1909: 108), commented upon a “colony” of Rough-wings in Oakland County, Michigan, in 1901, which contained eight nests, and other “smaller” ones in the same place in subsequent years; but otherwise described the species as not colonial in its nesting. Stone (1894: 139), writing of the pine barrens of New Jersey, reported all the “colonies” which he had examined proved to be of Rough-wings. Lincoln (1920: 73) mentioned colonies, in Colorado, of up to 150 birds. Low (1945: 132) described, in Idaho, a colony of 300 pairs, about equally Bank and Rough-wing. The association of the Rough-winged and Bank Swallows is described in a large number of published accounts; but the majority of cases involve only a single pair (cf. Bergstrom, 1953) or at most a few pairs (cf. Saunders, 1914: 140) of Rough-wings, in or at the edge of a colony of Banks.

Although occasional large aggregations of Rough-wings might be regarded as additional evidence of the birds’ excavating, there is little in the published accounts by which to judge. Perhaps these assemblages owe their existence to abandoned Bank Swallow sites, or to an abundance of existing holes of some other origin.

My evidence all tends to show that the Rough-winged Swallow in southern Michigan is not colonial. At no time did I have more than two or three active nests under observation in an immediate vicinity, and my closest simultaneous nestings (in Tubes 1 and 15) were about 14½ feet apart. Tube 16 was placed about 3 feet to

the left of Tube 8, and Tube 17 about 8 feet to the right; and during two seasons only one of the three was occupied at a time.

GEOGRAPHIC EFFECTS

It appears that topography, degree of human disturbance, and other variable factors influence the availability of nesting sites; but there seems little geographic difference in the responses of the birds themselves. In the hilly country of the East, the Rough-wing is predominantly a bird of rocky gorges, shale banks, stony road cuts, railroad embankments, and similar situations (cf. Eaton, 1914: 352-354). In the Midwest and West where such places are rare or lacking, the birds more often find suitable conditions in gravel pits, eroded margins of sluggish streams, and other such exposed banks of sand, dirt, or gravel. Always, locations about bridges, buildings, and other man-made structures seem to be acceptable. The Rough-wing may show a stronger tendency toward colonial habits in the more arid and sparsely settled western part of the range. This, however, may be dependent upon increased abundance of the species, combined with greater concentration of nesting sites. The note by Low (1945), for example, describes the remarkable density not only of Rough-wings, but of several other hole-nesting bird and mammal species as well, in a particularly favorable spot.

GENERAL ADAPTABILITY

It is often stated that the Rough-wing commonly, or even "invariably" (Todd, 1940: 369) selects a site near water. This seems to be generally the case; but I myself have seen nests that were located from a few hundred yards to half a mile or more from any water. I have been unable, from observation or reading, to define any limiting factors, in the way of height, depth, direction, or exposure, in the Rough-wing's selection of sites.

Many published accounts have called attention to the Rough-wing's indifference to continued disturbance. Stannis (1879) wrote of several pairs nesting close beside a railroad west of New Haven and not disturbed by the passing trains. Brandenburg and Campbell (1935: 241) listed the Rough-wing as one of the few species that showed no decline when a section of stream was cleared and drained, though the bird population as a whole dropped by 87 per cent during the period covered. I did not find the birds sensitive, at least in the advanced stages of nesting, either to my periodic inspections or to normal operations in the gravel pits.

ARRIVAL ON BREEDING GROUND

As there is little in the published record pertaining to the Rough-wing's behavior before nest building, even a preliminary survey is of some interest. Much remains to be worked out by one in a position to make prolonged observations upon the newly arrived birds, with techniques for marking numbers of them and charting their behavior.

Rough-wings have in my experience begun to make their appearance around the nesting areas during some mild spell in the last third of April. Movements of the earliest arrivals are always extremely erratic, so that accurate year-to-year comparisons are difficult to make. But each spring the birds were present in good numbers by the first of May. Allen and Nice (1952: 617) found "males usually in the majority" in the first Purple Martin flocks to arrive. This seems to some extent to be true of the Rough-wing, although certain observations early in the season have indicated that both sexes were very shortly present.

Early behavior. The Rough-wing's actions suggest from the start an admixture of sexual or territorial aggressiveness with tolerant sociability, which seems to characterize their relationships throughout the breeding season. Immediately after arrival the swallows begin to show spasmodic interest in nesting sites. Individuals of both sexes hover close in front of available cavities, call, perch occasionally at the entrances, at times actually enter for a brief period, and sit watchfully close by. In sections with no suitable holes available, they are often seen coursing back and fourth along the banks, swooping close to hover momentarily and investigate any slight crevice or depression. There is sporadic and more or less violent bickering from the outset, and frequent wild pursuits back and forth over the pits. Such pursuits, which may involve several birds, at the beginning of the season show little or no obvious relation to the forthcoming breeding activity. The birds spend much of their time feeding (their insect food being, of course, still scarce), often over the fields and ponds at a distance. During inclement weather, attention to nesting territories may cease altogether.

AVAILABILITY OF SITES

At the time the first Rough-wings arrive there are generally a few nesting holes already available. In my area an occasional kingfisher or Bank Swallow burrow of the previous season always escaped total obliteration. Belted Kingfishers (*Megaceryle alcyon*) began excavating early enough for a few of their fresh and unfinished burrows to provide possible sites. Judging by my observations of 1950, however, the places initially available could not provide for more than perhaps ten per cent of the breeding Rough-wing

population in such an area. (In subsequent years, the nest tubes I had already installed provided a large additional source of nesting places accessible at any time — an artificial element, yet quite consistent with conditions, say, along a perforated retaining wall.) More significant in the Rough-wings' nesting economy seem to be the sites that are provided at some time after their arrival. Kingfishers continue to dig (and often abandon) burrows at scattered points. Bank Swallows arrive (in this area commonly a few days after the Rough-wings) and immediately begin excavating. Cavities may be left at any time by miscellaneous human activities, by other animals, or by physical agencies. In the case of the present study, I continued to install nest tubes at irregular intervals up to mid-May and even later.

Delayed nesting. For a very large segment of the population, the observed behavior can only be interpreted as "waiting" for an indefinite period, in favorable areas, for nesting opportunities to present themselves. The promptness with which such birds accept newly provided cavities, as the season advances, is in marked contrast to the deliberate behavior of those with access to suitable sites from the first. A pair or so of Rough-wings will almost invariably be present at each sizable Bank Swallow colony, from its earliest inception, and ultimately locate an acceptable spot. I have also regularly observed them about any fresh kingfisher diggings in evidence.

The attraction that fresh digging of any description holds for the Rough-wing has been inescapably evident. The circumstances of the installation of my nest tubes made their acceptance interesting and significant. I set all of the tubes into banks, and all were first put in place *after* the arrival of Rough-wings in the pits. I chose a variety of sites: some at points where birds had been seen, some selected purely at random, and a few deliberately chosen as unlikely spots. In at least eight cases Rough-wings were circling close, considerably excited, as I worked. In three cases from one to four of the birds were seen to hover close beside a partially completed hole as I stepped back before finishing the work of installation. At Tube 14 there were two hovering, perching, and calling at the entrance just two minutes after I left (about 8:50 a.m., May 7, 1951), and nest building was going on by evening of the same day. About nine newly installed tubes received close attention within less than an hour of the time I finished; and about eight additional ones seem to have been accepted within a day of their installation. Nests were completed or partially built in 19 of the 21 tubes the season they were installed. In all cases the Rough-wings involved had evidently been in the vicinity for periods ranging from a few days to possibly three weeks, or even more. An occasional instance might have represented a second nesting attempt;

but this was not generally the case. The birds, apparently, simply postponed nesting until a ready-made site was found, even if this was not until egg laying had commenced in other nests. As the season advances some individuals may lose the urge to nest, without ever having made a start. The recurrent appearance of unaccounted-for individuals throughout each nesting season has led me to suspect that a considerable population of non-breeding Rough-wings is present, not attached to any territories.

TERRITORIAL BEHAVIOR

As in most swallows (cf. Emlen, 1952: 190, and 1954: 29-30; Allen and Nice, 1952: 617-618, 657; Kuerzi, 1941: 12; Shirling, 1935: 193-194; Davis, 1937: 68; Petersen, 1955: 240-241; Lind, 1960: 52-53), the concept of a "breeding territory" in the case of the Rough-wing seems applicable only to the nesting cavity itself and its immediate vicinity. The significance of this sort of territory, and its selection and defense, in a hole-nesting flycatcher, is discussed by Haartman (1956).

A male's habitual frequenting of a site, with continued perching, hovering, and calling in the vicinity, proclaims it as his territory. There is, however, great fluctuation in the vigor and constancy of defensive reaction. I have often seen three or more Rough-wings remain for a time, perched or hovering, within a yard or less of a nest, with little or no visible sign of conflict. At other times the arrival of an outsider close to the same nest touches off violent pursuit and fighting. As nearly as I have been able to determine, individual females establish their right to definite nest sites more or less independently of (and probably after) the males, and thereafter both birds share in the rather sporadic defense of the site (cf. Allen and Nice, 1952: 617-618; Petersen, 1955: 240-241). Displays of territorial squabbling continue intermittently, though with diminishing frequency and vigor, until the young leave the nest.

The male has a tendency to use a favorite perch in the vicinity of the nest site, or several such perches, as vantage points from which to maintain his territorial rights. The perch itself, however, is not defended. I have noted at least one instance of perches (in a pile of cut brush) being used intermittently by members of two, and probably three pairs. Even when perches are only a few feet from the nest, there seem to be no defensive reactions until an intruder approaches the entrance itself.

The male of Nest 73a apparently kept up the defense of a territory even after a first mate was lost, during the unsuccessful nesting (73b) by a second female in the same tube, and until an abortive third nest building (No. 93) was finally abandoned. Beyond, I remark upon

the tendency to use the same cavity a second time, or to move only a relatively short distance, in the event a first nesting is interrupted. Blake (1953: 107) suspects (from behavior traits) that the same male nested in a bank at Cambridge, Massachusetts, each summer from 1947 to 1949, although females caught and banded at the nest were different birds each season. I too have suspected, though I can offer no proof, that certain males returned to the same territories on successive years. One female (No. 50-11129), marked and banded in 1951 at my Tube 12 (Nest 72), deserted and immediately renested (87) in the adjacent Tube 20. In 1952 I again caught and examined this female, once more nesting (108) in Tube 12. Thus females and probably males, at times, use a site for more than one season.

Evidently, under strong stimuli, the territorial barriers can break down completely. This was shown during a spell of very cold, wet weather in 1951, when I captured four Rough-wings (one female and three males) huddled in my Tube 6 (Nest 67) and the following day four (three females and one male) in my Tube 14 (Nest 73).

Defensive reactions. Several orders of defensive behavior are recognizable. The first is represented by the special call the male utters when close to his nest site. It is almost invariably given whenever another individual (of either sex?) passes. This note might thus be regarded as a territorial "song." If the possible intruder continues on its way, there is usually no further demonstration.

Another mild warning reaction, which I have seen used on two or three occasions while birds were perched, is an open-mouthed threat display, in which an individual crouches slightly and extends the head toward another, the bill gaping. I am not sure whether this is used by both sexes or only by the female, perhaps as a deterrent to unwelcome courtship attempts. Emlen (1952: 180, 190) mentions an apparently similar gaping threat used by Cliff Swallows.

Under certain conditions, close approach to the hole by an interloper will provoke an actual attack by either or both of the defending pair. In some cases the visitor will promptly leave at the first swoop in its direction, and the attack will not be pressed. Often, however, a spirited chase will develop. The original occupant (usually the male) appears always to be the aggressor, and so far as I have been able to determine, the victor in any struggle to follow. At times pursuit gives way to actual fighting, when the two contestants face each other, hovering a few inches apart, and rise, sometimes twenty or thirty feet into the air, sparring as they do so. Several times I have seen other individuals successively join the fray, until four or five are briefly involved — and it is impossible to determine the outcome of the original controversy.

In extreme cases the birds come to grips, and may fall to the

ground still clutching each other with bills or feet. I have observed this on a few occasions, and always the birds have separated soon after reaching the ground. Webster (1915), however, observed two that "grappled each other and fell to the road-bed where they lay sprawled out motionless, with outstretched wings and tail, occasionally giving a flop when they took a firmer hold with their beaks, which were buried in each other's breasts." Van Tyne (unpubl.) described to me the actions of two Rough-wings he found close to a nest (my No. 86), May 16, 1951, apparently fighting, one grasping the other by the neck as they dropped to the ground. He was able to pick them up (the birds continuing to cling a moment in his hand) and to carry them home for banding. He concluded from the comparative development of the primary serrations in these two that they were a male and a female. It appears, nevertheless, that such displays of violence are more probably territorial than sexual in nature. Comparable struggles seen among Bank Swallows are variously regarded as part of the courtship activity (Gross, 1942: 401-402) or as territorial fighting (Beyer, 1938: 123). Similar fights among Tree Swallows, often involving a female and a male (Kuerzi, 1941: 12-14), among Cliff Swallows (Emlen, 1952: 192), and among Purple Martins (Allen and Nice, 1952: 617-618) are described as a part of territorial behavior.

COURTSHIP AND MATING

The choice of mates probably involves merely a male and a female establishing themselves at the same site and tolerating each other's presence there. A parallel situation in Cliff Swallow behavior is described in detail by Emlen, who refers (1954: 27) to a "relationship of mutual tolerance [at the nest site], . . . which was the pairing bond." From the first appearance of a pair of Rough-wings at a potential nest site, they are seen constantly examining the cavity together and perching very close to it side by side, whereas the close approach of any other individual will normally evoke the defensive behavior just described. Sometimes it seemed that the male was in possession for a time before any female was in evidence; but in other cases, particularly later in the season, the two members of the pair seem to arrive nearly at the same time (perhaps actually together), and ready to proceed with nesting. How much the selection of partners is directly influenced by the chasing and fighting, or by special courtship performance or display, remains uncertain. No well defined sequence of pair-formation "ceremony," as described, for example, for House Martins (*Delichon urbica*) by Lind (1960: 55ff.) has been discernible.

Flights and fighting. Pursuit flights are a conspicuous element of

Rough-wing behavior. These range from a mere following of one bird by another a few feet behind, to the most violent of headlong chases. Most often, the actual beginning is not observed. Such flights may cover hundreds of yards, extending back and forth across the pits, around in wide circles, high into the air, and close along the ground. They end, about equally often, with some actual fighting, with the chase simply abandoned in mid-air, or with the participants (apparently tired by their efforts) perching amicably side by side.

From instances in which I have had a basis for distinguishing the sexes and recognizing individuals, I conclude that several functions are here served by grossly similar patterns of behavior (cf. Haartman, 1956: 465). Most of the really fierce pursuits, and those involving fighting, seem to be concerned with territory or with fighting between rival males. Flights in which a single male was seen to pursue a female, while often prolonged and at times spirited, were apt to be of a more leisurely nature; and on a number of occasions both birds would finally alight together. This type of flight, like the sexual chase of Bank Swallows described by Petersen (1955: 241-242) seems "clearly an activity of mated birds" (cf. Tinbergen, 1939: 21-22). The frequent and vigorous participation of extra individuals, however, renders any of the pursuits exceedingly difficult to interpret.

Display. Grinnell and Storer (1924: 503) have described the display of the male Rough-wing as follows: "From time to time the males were seen in pursuit of the females. . . . They would spread the long white feathers (under tail coverts) at the lower base of the tail until these curled up along either side of the otherwise brownish tail. The effect produced was of white outer tail feathers, much as those of the junco or the pipit." The display is frequently seen wherever groups of Rough-wings are under observation, and is a somewhat startling phenomenon when first noticed. Apparently the spreading of the feathers is to some extent under voluntary control, for it is conspicuous only intermittently, and appears to be independent of the wind, and of the speed and direction of flight. It is not, however, employed only during direct pursuit of a female: I have seen two males passing, both flashing white coverts prominently; and have on other occasions seen the white areas clearly when solitary males passed me. The exact function of the display is not clear; but it seems probable that it is a means of sex *recognition*, rather than a courtship display as such. It is clearly a mark that would be visible from behind and above, not from the front. Occasionally a hint of coverts spread in comparable fashion was seen on birds known to be females. This, together with the fact that the flash of white can be an extremely transitory thing in the males, makes me hesitate to subscribe to the statement (Grinnell and Storer, *loc. cit.*) that "males can by

means of this trick be distinguished from the females at a distance of fully 50 yards'' — though, if fully displayed, the white patches are visible at even greater distances.

Pursuit of building female. Another performance I have observed on a few occasions, which I believe to be of special significance in courtship, is a male's continuing pursuit of a female carrying a trailing bit of nesting material. I have particular notes on five occurrences, at four nests, and several facts seem significant. First, the material carried was in every case a conspicuously long, flexible piece, such as would normally be used in *lining* a nest. Each of the occurrences, except one, was known to take place during the final stages of building, and from one to five days before laying commenced. In most cases the female did not go directly to the nest with the material, as she commonly does, but was seen to fly back and forth and circle. The male's interest in the procedure was obvious, and his response quite different from his usual casual accompaniment of the building female. While the exact significance of this behavior is obscure, the inference is that it is regularly associated with the later stages of courtship, perhaps as a sort of stimulus to copulation itself.

Copulation. I have never been able to observe the actual act of copulation by Rough-wings, or to learn anything of the behavior leading up to it. Perhaps this takes place in the nest, even though the male is seldom seen to enter it. In Tree Swallows (Kuerzi, 1941: 19-20), and Purple Martins (Allen and Nice, 1952: 621) copulation takes place in the open. According to Stoner (1936: 181), Bank Swallows copulate in the open; but Petersen (1955: 243) concluded they must do so in the burrows. In Cliff Swallows (Emlen, 1954: 31) "complete copulations regularly occurred on the nest and were never observed elsewhere." Kuerzi (*loc. cit.*) reports copulation as beginning from five to six days before the laying of the first egg. Allen and Nice (*loc. cit.*) go on to say that in the Martin it "ceases with the laying of the first egg." Among Cliff Swallows it was seen (Emlen, *op. cit.*: 32) as late as "the afternoon preceding the laying of the last (fourth) egg."

NESTS AND NEST BUILDING

DESCRIPTION

Rough-wing nests have been characterized in the literature as "loose, crude foundations" (Dingle, 1942: 427) and "shapeless heaps of rubbish" (Todd, 1940: 370). The foundation below the nest proper is indeed little more than an indiscriminate pile. But in my experience the cup itself, in new nests, has been well shaped and neatly, if often somewhat loosely, lined with finer and softer materials. I think that some descriptions may have been based on nests dragged roughly

from a deep tunnel, or examined after departure of the young (when nests are always heavily trampled).

The nest may be, as Dawson (1903: 282) expressed it, "bulky or compact according to situation." I have generally found at least a handful of material in the average burrow. My Nest 1, built on the broad flange of a bridge girder, was of unusual size. Nickell (1949) seems to have recorded the largest, built on top of a tool cabinet in a garage, at Bloomfield Hills, Michigan, which was found to be "22 by 17 inches by 4 inches thick at the center. The dry weight was 435 grams." At the other extreme, Van Fleet (1876: 10) found a set of Rough-wing eggs on the bare sand of a burrow, with no nest whatever.

Materials. A wide variety of materials are used by the Rough-wing for nest construction. Dingle (1942: 427-428) has presented notes by a number of observers in various parts of the country. General statements appear in a great many standard reference works and shorter papers. The specific nature of the items seems largely fortuitous, and I shall not attempt a detailed listing. The bulk of the nest, however, is generally composed of some of the following: woody twigs, weed stems, straw, roots and rootlets, coarse and fine grass (either dry or green), sedges, leaves and parts of leaves (sometimes green), chips, bark shreds, plant fibers, pine needles, seaweed (Bailey, 1913: 262), moss, grass heads, flowers or parts of flowers, seeds, and miscellaneous bits of rubbish. Even within a limited area there may be great variation between nests, one being almost entirely of grass, and the next largely of stout stems and woody twigs. Many include a variety of material. The lining, at least, is usually of grass or other fine stuff.

Observers agree that the typical Rough-wing nest — in sharp contrast to the Bank Swallow's — is not lined with feathers. In ninety-odd cases I have not found a single feather that seemed to be part of a nest. Two nests (85 and 88) were built on top of abandoned House Sparrow nests, which as usual contained many feathers, and the old material was not entirely removed; but in neither instance were any of the feathers incorporated into the Rough-wing's lining. The neighboring Bank Swallow nests throughout the study were uniformly lined with numerous white feathers.

Many rather unexpected objects are worked into the foundation of Rough-wing nests. I have found a number of little bits of shale, a piece of wadded-up friction tape, and a bit of paper gasket. Dingle (*loc. cit.*) quotes from Dickey (MS) "shells of chicken eggs." Nickell (1949: 189) includes in his list strips of paper, bits of cellophane (this estimated at one per cent of the total weight), wooden match stems, and cigarette stubs. In the Ann Arbor area I have found horsehair in three nests. Nest 65 had one long piece coiled about the inside. Nests 59 and 60, both in a gravel pit away from my regular study area,

included a considerable quantity, woven well into the structure of the nests.

Extra material. Material placed within the nest after its essential completion is scarcely a part of it, although a positive distinction cannot always be made. The presence of green grass, green leaves, or other fresh vegetable material has received comment in the literature. Todd (1940: 370), for example, mentions "green leaves and petals from various trees and shrubs," and Harris (1921: 254) a nest (among those of Bank Swallows) "lined with petals instead of feathers."

From periodic inspections, I have concluded that most green materials, principally the grass blades, constituted a final touch to the nest lining itself; others, however, were added some time after the rest of the nest had been completed. I have notes on the appearance of such items in 13 nests, about 14 per cent of those studied. Small leaves (in one case those of sweet clover), green grass blades, a bit of small composite blossom (everlasting?), and a piece of material resembling thistle-down, were found. In four instances the material must have been added late in incubation; but in all others it appeared shortly before the eggs were laid, or during the laying period. The quantities were always small, and repeated additions were not detected in any nest. I can offer no support of the statement, quoted from Dickey (Dingle, 1942: 428) that "the parents supply broods daily with beds of fresh green leaves," and that "soiled leaves are removed, with the dung." I am sure nothing of the sort happened in the nests I studied closely.

Allen and Nice (1952: 622-623) discuss at some length the use of green leaves by Purple Martins (cf. also Raynor, 1959), a habit that appears analogous to that of the Rough-wing, but far better developed. Suggested functions of the behavior, variations of which occur in birds of other families, are quoted by the above authors from a number of sources, and include concealment, cooling, and humidifying. Tree Swallows (Weydemeyer, 1934: 102) and Bank Swallows (Stoner, 1936: 193-194; Petersen, 1955: 250-251) continue to add feathers to the nests during laying, incubation, and brooding; the Violet-green (Edson, 1943: 397) does so at least during laying.

Another statement of Dickey's, quoted by Dingle (1942: 428), is the only reference I have seen to the use of fresh horse or cow dung: "A number of nests curiously contained moist horse dung; we wonder why. Perhaps the vile smell tends to ward off vermin." Substantial quantities of such material as dung could scarcely fail to improve the insulation of the otherwise loose and porous nest-lining, but I doubt if the effect would be significant. I have noted the occurrence of dung in 13 (14 per cent) of the nests observed.

Only two of the nests in which added leaves were found also contained dung. In some instances small pieces of the material were loose in the nest; but more often it was smeared over the lining and on the eggs themselves, occasionally (as in Nest 22) copiously. I usually first noted this after incubation was well along, but in Nest 69 small bits of the excrement appeared as soon as laying was complete, when incubation had not begun. I captured a female May 16, 1952, on a nearly completed nest (107), which had her bill heavily smeared with dried dung; none was visible in the nest.

PREPARATION FOR BUILDING

Nest building may follow immediately, or be delayed for several days, after a pair has established itself at a nesting site.

There are reports that the Rough-wing sometimes cleans out a cavity before building a nest therein. Blake (1907: 104) indicated that a pair in Vermont, nesting in 1906 in a hole also occupied in 1905, "cleaned out and relined" the cavity the second year. Tyler (1913: 93) considered that holes he observed in California were "thoroughly renovated" before occupancy, on the basis of the piles of debris below occupied burrows.

Generally speaking, I have found no appreciable amount of renovating before nest building. Nest 88 was superimposed upon a deserted House Sparrow nest with the clutch of five eggs intact. Nest 59 appeared to have been built on top of an older Bank Swallow nest, with at least two eggs. Nest 86 (1951) seemed to be built on the remains of Nest 44 (1950). Sometimes I cleaned out the mass of old material, or part of it, from my nest tubes. Sometimes I left the remains of the previous nest undisturbed. In 1951 and 1952 the Rough-wings showed some preference for newly set tubes, or for ones that had been thoroughly cleaned. Where mice or other small mammals had stuffed the nest chamber quite full of soft material during the winter, I never knew the swallows to reoccupy the site until I had removed at least part of the sodden mass. When the nest chamber was only partially full, the birds accepted the site freely, and proceeded to build again on top of whatever the cavity contained. The amount of new material added tended to be in inverse proportion to the old remaining. In extreme cases the new nest consisted of little but a grass lining, placed in a hollow of the packed-down old material. For Nests 73b and 107b, at least, a second individual seemingly took over a partially finished nest, abandoned for a time, and completed construction. An abnormal second nesting (Nest 87) took place after the addition of no more than a few wisps of grass to the lining of Nest 78, completed by another bird about a week before and abandoned before any eggs were laid.

In all of these situations, the Rough-wings either incorporated any existing material into the base of the new nest, or disregarded it altogether. While they often appeared to move it about to some extent in the chamber, there was nowhere any evidence that any had been removed.

BUILDING

There is little published information about the Rough-wing's building activities. Mearns (1878: 46) watched a pair near West Point, New York, "while they constructed their nest, during which time they were often seen to alight close together, on a board-fence from which they descended after the rough materials of which the nest was composed." Emilio (1929) describes an attempted nesting at South Middleton, Massachusetts, and mentions "two birds carrying sticks, presumably for nesting material." In Nickell's account he refers (1949: 188) to "2 Rough-winged Swallows . . . presumably a pair . . . carrying nesting material." It is not surprising that all three of these notes mention the activity of two birds; but it is doubtful whether in such cases both members of the pair actually *carried* material.

Roles of sexes. I have watched spells of nest building at about 17 nests, and the behavior has always been about the same. The material is gathered from the ground, usually in more or less open and level spots, but not uncommonly from the sloping pit walls as well. Nearly always both members of the pair have been together, but in nearly every case the female has been judged to be doing all of the actual gathering and carrying of material. The male commonly accompanies the female on her trips, alighting beside her as she picks up material. When she flies to the hole, he often follows her to the entrance, then continues to circle, veers off and alights on his accustomed perch, or occasionally goes in after her. At other times he remains at the collecting point, or simply stays on his perch, while the female continues to fly to and from the hole. At all times he maintains an appearance of alert attention, calls frequently, and fights or pursues other males that too closely approach either the hole or the female.

I have seen males make spasmodic efforts to pick up nesting material while close to the female; but they have always either failed to get a grip, and not continued the effort, or immediately dropped whatever they picked up. If the male takes any active part at all, I think it is apt to be during the early stages of nesting, and may function more as a stimulus to the female, than as a significant contribution in itself.

Both sexes of the Bank Swallow (Petersen, 1955: 250; Stoner, 1936: 193), Barn Swallow (Wood, 1937b: 96; Smith, 1933: 414), and

Cliff Swallow (Gross, 1942: 472, 474; Emlen, 1952: 185, and 1954: 28ff.; Vietor and Vietor, 1912: 150) cooperate in building. This is true also of the Purple Martin (Allen and Nice, 1952: 620-621) although the male's interest declines as building progresses. A male Violet-green Swallow was described by Combellack (1954: 437) as assisting to a limited extent. In the Tree Swallow, apparently, the male sometimes helps (Kuerzi, 1941: 19) and sometimes takes little or no part (Weydemeyer, 1934: 102). For swallows in general, Skutch (1960: 282) concludes that "the nest is as a rule built by both sexes."

Behavior. In gathering of nest material, the only activity in which Rough-wings normally move about on the ground, they do so jerkily, but with surprising rapidity. The ordinary gait is a shuffling walk; but at times they make little hops, and very short flights, seeming more nervous and excitable than usual. They seek material close to the nest, and return time after time to the same approximate spot. When the foundation is being built, there is a tendency to pick up the bulkiest item within reach, even if it proves much too large to carry. I saw one, during the first day of building at Nest 24, try to pick up a stick over a foot long and as large as my little finger. The birds show little persistence, however; if a few quick trials do not suffice, they at once turn their attention to something else. Often, an individual simply abandons the effort for the moment and flies off with nothing at all. When gathering dry grass, however, the females make more determined efforts, grasping a rooted piece and worrying it with considerable vigor; this must often be necessary in obtaining the green materials frequently used, though I have never observed that process. Grass, like the coarser material, is often selected in very long and unmanageable pieces.

The habit of gathering large and awkward items, and then dropping any that do not go easily through the entrance, commonly results in the scattering of a great deal of material below the nest opening. This is so characteristic as to be of great assistance in locating Rough-wing nests.

Wherever there are holes not immediately taken as regular nesting places, there are nevertheless likely to be small accumulations of Rough-wing nesting material. I do not recall that more than one or two of my nest tubes, during any of the three years of my observation of them, failed to receive at least a few tentative sticks or straws, and often quite a heap of material was built up in those not used for actual nests. In countless little crevices, I have found what I suspected were the result of abortive building activity by Rough-winged Swallows.

Duration. The process of building is commonly a protracted affair. There may be intervals of up to several days during which little or

no progress is made; or material may continue to be added slowly, but more or less constantly, until the nest is finished. A common pattern involves rapid building of the bulk of the foundation in two or three days, then a lag, and finally another spurt of activity during which the lining is added. I have known a few nests, however, principally (but not always) for late or second layings, which were built with great dispatch and with no evident interruptions. The periods of building are in themselves sporadic, and the work seldom goes on continuously for more than a few minutes.

The activity seems greatly influenced by weather conditions. Observations on a number of days have indicated that brief periods of sunshine and cloudiness resulted respectively in increase and decrease in nest-building activity by a number of different pairs, and by Bank Swallows as well as Rough-wings. Certainly the weather conditions over a period of days are an important factor. Particularly cool or wet periods have evidently caused suspension of work on most of the nests in progress, in addition to delaying the beginning of others.

In Table 2, I have summarized data on the approximate building times of 50 nests of 1950, 1951, and 1952 which seem relatively dependable. For 1950 my figures are nearly enough accurate to justify the calculation of a mean time: about 6.2 days for the 14 nests. For 1951 the mean of the seven most dependable figures only is 7.0 days. In 1952, for which generally longer periods and greater variability are shown, building was notably slow and irregular. It began early and then was abnormally prolonged, even in some of the later nestings, by cooler weather.

TABLE 2
DETERMINED AND ESTIMATED TIMES OF NEST CONSTRUCTION
FOR THREE YEARS OF OBSERVATION*

	Days of Construction																	
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1950 Nests	1	1	3	3	3	2	..	1
1951 Nests	..	2	1	1	3
	(1)	..	(4)	(4)	(2)	(1)
1952 Nests	(1)	(2)	..	(5)	..	(2)	(1)	(2)	(1)	..	(2)	(1)

* Figures not in parentheses are correct to about the nearest day; those in parentheses are based to some extent upon inference, particularly for the year 1952, but are adequate for general comparison.

In general it can be said, from Table 2, that nest building requires an average of a week, or somewhat less. In certain cases this is reduced to as little as three days; or it may extend to about 15, or even to 20 days.

Kuerzi (1941: 18) found the nest building of Tree Swallows to range between one and three weeks. He describes great variability, and remarks upon the "cessation of nest building during cold days" (cf. also Paynter, 1954: 36). Weydemeyer (1934: 102) gives an average of 29 days for the building time of 37 Tree Swallow nests. The Violet-green Swallow (Edson, 1943: 397) also has a "variable" nest-building period, of "sometimes a few days and again many." The Purple Martin (Allen and Nice, 1952: 619) requires "three to four weeks." Thus the time required by the Rough-wing for building is by comparison with these other species not surprising.

Part III
EGGS AND INCUBATION
EGGS

CHARACTERISTICS

The eggs of the Rough-wing are immaculate white, as apparently are those of all other swallows except the Barn Swallow group (*Hirundo*), some species of *Petrochelidon* (the American Cliff Swallows and relatives), and the Crag Martins (*Ptyonoprogne*) of the Old World (Mayr and Bond, 1943: 336; Bond, 1943: 117). Freshly laid eggs are translucent, and hence may have a slightly pinkish cast; but with incubation they shortly take on the "somewhat glossy" (Bent, 1942: 428) appearance referred to by various authorities. Their fragility was commented upon by Davie (1898: 413), who stated that "the shells are more tender" than those of the Bank Swallow. Addled eggs can often be recognized by the appearance of the half-visible contents, long before hatching time. Ray (1910: 21) wrote that "in the case of the Cliff and Rough-winged Swallow, we have both hard- and soft-shelled eggs in birds of the same family."

Shape and size. The eggs are "more elongate, as a rule, than the eggs of other swallows, usually elliptical-ovate" (Bent, 1942: 428), and somewhat larger than those of the Bank Swallow. Bent gives average measurements for 50 Rough-wing eggs, the localities not stated, as 18.3 by 13.2 mm. My own averages, based on measurements of 46 eggs from seven Michigan nests, and not differing greatly from other published figures, are 18.58 and 13.28 mm. Skutch (1945: 21; 1960: 268) gives 19.8 by 13.6 as the average dimensions of 27 eggs of *S. r. fulvipennis* from Costa Rica and Guatemala.

The four extremes given by Bent (*loc. cit.*) are all beyond the range of my own measured sample, his maximum and minimum lengths being 20.6 and 16.5 mm., and extreme widths 15.0 and 12.2 mm. I have been impressed, however, by differences in size and shape that are evident in the field. In at least two sets the first-laid egg was markedly elongate. I have seen also a number of conspicuously small eggs, occurring either early or late in laying sequences.

In an effort to find some regularity in the variation, I measured with dial calipers the eggs of seven marked clutches (those upon which the figures above were based, most of them *not* showing abnormal differences). With length plotted against width for each egg, as in

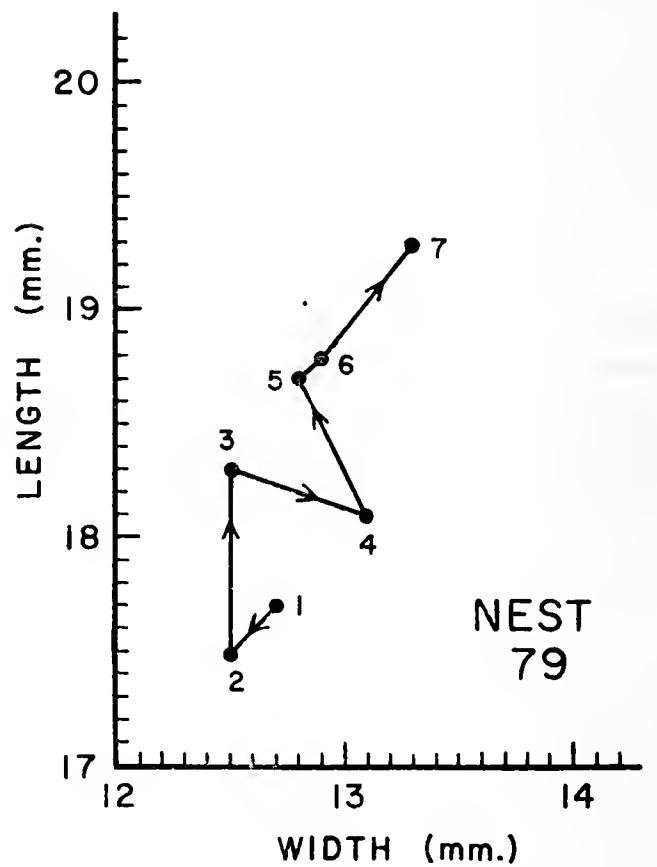
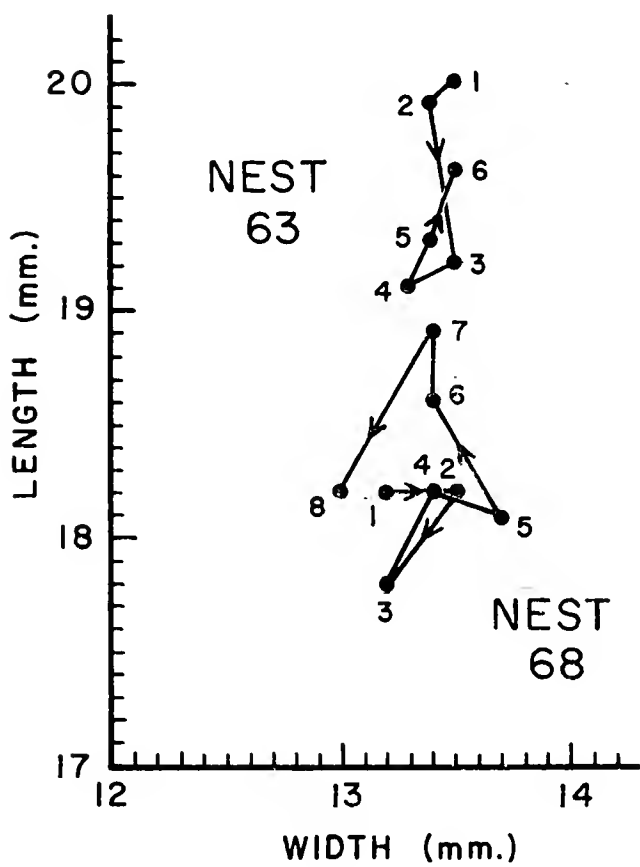
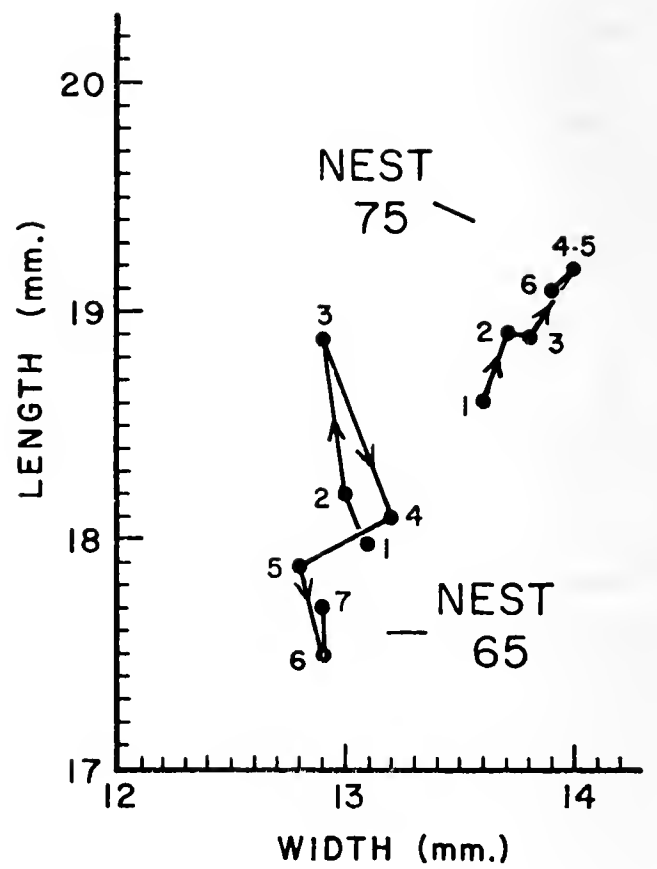
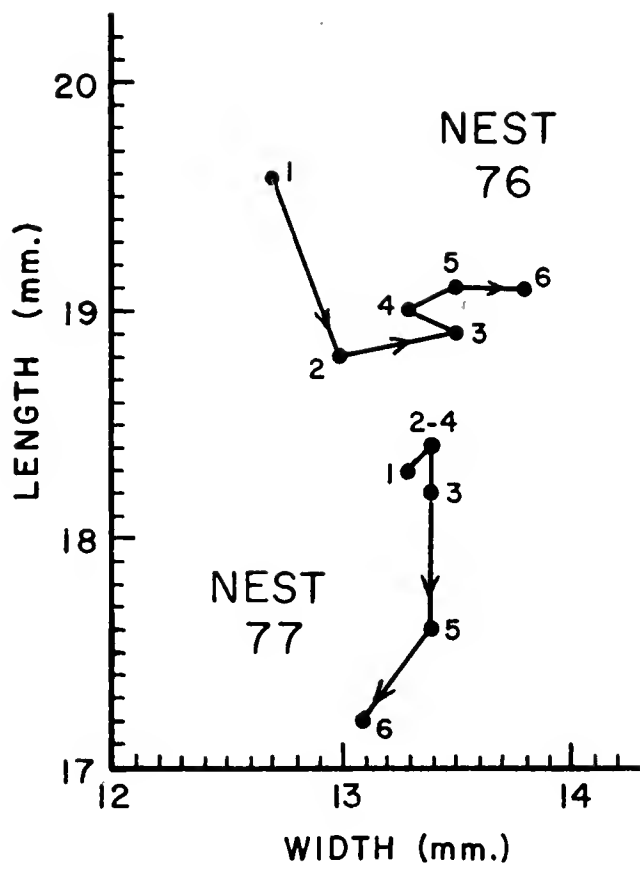


FIGURE 3. Measurements of Rough-wing eggs, to show variational trends among eggs of seven marked clutches.

Figure 3, and the resulting points connected in the order of laying, any trends during the course of laying become apparent. However, the diagrams for these few sets show no prevailing pattern. Perhaps simple dimensions do not adequately tell the story. More refined methods (cf. Preston, 1953) might well show significant changes that my simple comparisons have missed entirely. The importance of such factors as age of the laying female and size of clutch remains quite obscure. The very absence of any apparent regularity seems noteworthy in itself.

Weight. Hanna (1924: 151) gives the average of 14 fresh Rough-wing eggs (from California?) as 1.77 gm., with extremes of 2.00 and 1.66 gm. Two eggs of about average size, from one nest, I found to weigh 1.8 and 1.7 gm. respectively, on the day before hatching. Presumably they had lost weight during incubation; Hanna (p. 146) found that "as incubation advances eggs become lighter in weight . . . as much as 11 per cent" (cf. Lack and Lack, 1951: 513, where data on 12 Common Swift [*Apus apus*] eggs showing an average loss of 17 per cent are given). If we can judge at all from measurements, it was *not* true in my sample, as with Purple Martin eggs (Allen and Nice, 1952: 624), that "the first egg was always the lightest and usually each thereafter weighed a little more than the one before."

THE INTERVAL BEFORE EGG LAYING

Consistent with the prolonged process of nest building is the period that normally elapses between the completion of the nest and the laying of the first egg. As was pointed out, the adults are commonly not in evidence. In extreme cases the nest may take on a slightly loosened and unkempt appearance, which is in some instances corrected by a few last-minute additions just before laying. Considering the difficulty of determining exactly when the nest can be regarded as complete, it is hard to estimate the duration of the time lapse. In 35 instances my data are complete enough to give a figure accurate within a day or so; and in others fair approximations are possible. Table 3 summarizes my information on the point. In 1950 the mean duration of the lag was about 3.5 days, while in 1951 it was a little over 5.5 days. In both these years the modal time was between three and four days. Weather conditions were generally favorable during the critical part of the 1950 season. All of the 1951 nests showing a lag of eight or more days were completed before a severe spell of cold and rain on May 10 and 11, the others not being finished until equable conditions prevailed. Estimates for the 1952 nests do not justify calculating a mean value; but they indicate lags similar to those of 1951, there having been again some periods of inclement weather to delay the normal cycles. It is thus seen that excessive delays before egg laying

TABLE 3
ESTIMATED TIMES BETWEEN COMPLETION OF NEST BUILDING
AND BEGINNING OF EGG LAYING*

	Interval in Days													
	0	1	2	3	4	5	6	7	8	9	10	11	12	13
1950 Nests	..	1	..	7	7	2
1951 Nests	1	..	2	4	4	1	1	1	1	1	1	1
1952 Nests	(1)	(2)	(4)	(2)	..	(4)	(1)	..	(1)	..	(1)	(1)

* Figures not in parentheses represent estimates correct to about the nearest day; those in parentheses are approximations, less accurate but adequate for general comparison. (See text for discussion.)

are due to external influences, particularly to unfavorable weather conditions. Weydemeyer (1934: 103) writes of the Tree Swallow in Montana: "The time at which egg-laying commences depends somewhat on the weather. . . . Some nests have been completed for more than two weeks before receiving the first egg." However, there remains for the Rough-wing a minimal lag after building is completed, averaging three or four days even under ideal conditions. The single case in 1951 in which there seemed to be no demonstrable interval before laying (Nest 87) was a second nesting attempt after interruption of the laying of the first clutch.

SIZE OF CLUTCH

Clutches of the Rough-winged Swallow vary in number of eggs from three (Barrows, 1912: 553) to eight. Commonly stated ranges are four to eight (e.g., Bent, 1942: 428; Forbush, 1929: 161), or four to seven (e.g., Roberts, 1932: 44; Todd, 1940: 370); and five to seven eggs are generally given as the normal number.

My observations furnish more precise data applicable at least to southern Michigan. I have never encountered a clutch smaller than four, and have notes on only two apparent four-egg clutches (Nests 5 and 113). In both of these instances my observations were scattered, and the histories consequently open to some question. On the other hand eight-egg sets are of fairly regular occurrence. The nestings for which I can with reasonable certainty state the total layings number 61. Of these, 12 had five eggs, 26 had six, 19 had seven, and 4 had eight. The mean clutch size is thus $6.25 \pm .108$, with a standard deviation of .843.

Of the five-egg clutches observed, three were presumed to have been second layings, after known first clutches were lost; six others were begun later than the first of June and could reasonably be supposed also to represent second attempts. Only in three cases (Nests 25, 29, and 34) did five-egg sets probably represent first layings. More will be said later about second layings in general; but they represent a large proportion of the five-egg clutches.

Geographic effects. A general north-south gradation in average clutch size is indicated (cf. Lack, 1947: 303-306; Moreau, 1944: 308-312; Paynter, 1954: 137-138; Wagner, 1957). Oberholser (1938: 408) says of the Rough-wing (in Louisiana?) that "the eggs are usually about five." Howell (1932: 332) mentions clutches of six and of five eggs in Florida. Sprunt and Chamberlain, however (1949: 364), report "six or seven" eggs (for South Carolina?). The normal clutch of *S. r. fulvipennis* of Central America apparently does not exceed five eggs (Skutch, 1945: 21 and 1960: 268; Allen and Nice, 1952: 630). Even this is somewhat high for a tropical species (cf. Skutch, 1940: 503ff.).

No averages I have seen for clutch sizes of other North American swallows equal the figure I have calculated for the Rough-wing (cf. Weydemeyer, 1934: 103; Kuerzi, 1941: 24; Paynter, 1954: 39; Bent, 1942: 378; Stoner, 1936: 194; Petersen, 1955: 251-252; Allen and Nice, 1952: 624; Myres, 1957; Mayhew, 1958: 23). Indeed, among data available for species in other parts of the world, I have found no figures to indicate that the Rough-wing in the northern portions of its range may not lay, on the average, a larger clutch than *any* other swallow.

Averill (1933: 96), considering the Rough-wing a bird "of limited distribution, but with more than the usual number of eggs," finds it an exception to his rule that large clutch sizes characterize species of wide or Holarctic distribution, and says that "perhaps the peculiar choice of nesting site has something to do with this."

RHYTHM OF LAYING

One egg is normally laid on each successive morning until the set is complete. However, departures from this schedule occur, in the form of skipped days. I find 25 nests in which there was no doubt as to the day upon which any egg of the full clutch was laid; among these, five (20 per cent) show breaks in the regular sequence of laying. As it happens, all of these are included in Figure 4 (p. 65); and the patterns may best be seen by reference to it. Add to these many more nests for which I have incomplete data on laying, and of the resulting total of about 55 clutches there are nine (16½ per cent) in which irregularity could be proved or inferred. Both early and late, and

large and small, clutches have shown interruptions, though never one known to be a second laying.

Though exact data for swallow species are few, daily laying is evidently the general rule. Kuerzi (1941: 20-21) reported delays of from one to seven days in the laying of Tree Swallows. During a cold period, with little sunlight, "egg production fell to zero among nine laying females"; and afterward normal laying was resumed. Kuerzi also cites Austin and Low (1932: 41), who found lapses of two and four days in the laying of their Tree Swallows, but do not give details. Allen and Nice (1952: 624), in discussing Purple Martins, reported only one such irregularity: "when the temperature turned much cooler than normal, a late-nesting bird skipped a day between the second and third egg of her three-egg set." Lind (1960: 66) detected no correlation with weather conditions, in interrupted laying of House Martins.

With the Rough-wing the phenomenon appears unrelated to gross environmental factors. I have not recorded gaps in any two sets on the same day; and in all cases there were concurrent nests in which laying was proceeding without interruption. Days have been skipped even in the finest of weather. However, my records do not cover any extreme cold snaps during a laying period. Whereas a few apparent gaps could actually be due to some external disturbance, and represent eggs lost or laid elsewhere, most cannot be attributed to such causes.

Time of laying. As seems to be the general rule among small passerines, the eggs of the Rough-winged Swallow are always laid, so far as I know, in the early hours of the morning. During the laying period the female spends the night on the nest. In at least 14 recorded night observations upon eleven nests during laying, both early and late in the laying sequence, and in two cases on nights preceding days upon which no eggs were laid, I never found a nest empty. Nor have I ever found but a single bird (from all indications the female) present. In three observed instances the female has left the nest after daylight, and returned shortly to deposit the egg. I have examined nest contents at all times of day, occasionally at night, and frequently several times in a day; and not once in some 350 cases have I had any reason to suspect that an egg was *not* laid in the early morning. Despite the relatively frequent hiatuses in the daily laying schedule, none of these appear to involve any departure from the normal hour of laying.

I have found no such exceptions as have been reported for the Tree Swallow. Kuerzi (1941: 20) reports three instances in which a female laid two eggs in a 24-hour period; calls attention to the record of one such case by Austin and Low (1932: 41); and cites Shelley ("1934" — erroneously for 1935: 34), who records three eggs laid in a 24-hour period by one female. Paynter (1954: 38), however,

found complete regularity of laying in his Tree Swallow study. Allen and Nice (1952: 624) stated simply that Purple Martin “eggs are laid early in the morning” and evidently found no exceptions.

AGE OF FEMALE

Judging from the results obtained by others, some correlation is to be expected between the age of the female and egg laying, as regards both date and clutch size (cf. Lack, 1947: 313-314). Kuerzi (1941: 25) showed that laying dates were later for three female Tree Swallows breeding for the first time than they were for the same individuals the following season. Allen and Nice (1952: 624) found that four-egg clutches of the Purple Martin were “either second sets or were laid by the mate of a first-year male, presumably a first-year female.”

My data on this point are inconclusive. The females of Nests 88, 101, and 112 were judged to be first-year breeders by the presence of pinkish feathers in the chin. The female of Nest 92 had been banded (50-11437) the preceding summer as a nestling. Data on the laying of these four individuals are summarized in Table 4. The mean clutch size for the four is 6.0, or .25 below that found for my study as a whole — certainly not a significant difference for so small a sample. The second two nests were so extremely late that I strongly suspect they were second attempts — if this was *not* the case, then the delay is very interesting.

In Nest 104 (1952), where building was very long in progress, laying did not commence until May 29, and clutch was of only six eggs, the female was known by banding (50-11123) to be at least two, and probably three years old.

TABLE 4
DATA ON OBSERVED NESTING OF FIRST-YEAR FEMALES*

Nest Number	Female Known First-year by	Clutch of	Date of First Egg	Year	Remarks
88	pink in chin	6	(May 28,)	1951	Known second nest, but first laying
92	banded as nestling	6	(June 12,)	1951	Very late; may have been second try
101	pink in chin	5	(June 8,)	1952	Very late; may have been second try
112	pink in chin	7	(May 20,)	1952	About normal

* Parentheses around dates indicate uncertainty as to the day upon which the first egg of the clutch actually was laid; these dates are probably correct, and cannot in most cases be in error by more than one day.

DATES OF LAYING

The total laying period, as observed over three years of my investigations, extends from May 10 (1952) to June 25 (1950). Reference to Figure 18 (p. 117) will show at a glance the peaks of laying. Second clutches undoubtedly account for all of the very late layings; but the latest of the first sets merge, in the graph, with early second clutches. From this evidence, the peak of egg laying could be expected, in the Ann Arbor region, some time during the last ten days of May; and the majority of original sets would be complete by the end of the month. My data are consistent with the statement of Wood (1951: 289) that "eggs are commonly found [in Michigan as a whole] from the last of May to the last of June."

DESERTION

This is so closely associated with the processes of nest building, egg laying, and incubation, and particularly with second nesting attempts, that certain tendencies seem to warrant brief discussion. I count some 19 nests, among 98 on which I have data, which were deserted. That these represent about 19.4 per cent of the total is largely owing, I think, to my own activities, although in 1951 at least two nests (62 and 67) were apparently deserted as a result of inclement weather.

Relation to stage of nesting cycle. It is well known that birds in general are far more likely to desert during the early stages of nesting than after incubation has begun. According to Stoner, for example (1936: 224), digging into Bank Swallow holes is likely to cause the swallows to desert "unless the eggs are near hatching time, or the nest contains young."

During my work with the Rough-wing, 15 of 19 cases of desertion (79 per cent) occurred prior to the commencement of laying. I am not aware that merely looking into a nest, or examining the contents, ever caused birds to desert. Digging down to the nest cavity from above, in natural burrows, did not cause desertion in either of two cases, one (Nest 90) after the nest was built, and one (92) when the birds were just examining the site. Disturbance to the adult female, before laying has begun, is most likely to cause desertion. Out of four cases in which I merely opened nest tubes with birds inside, during building, there were two desertions. Twice, in natural holes, I forced the adult off the (empty) nest, and one of these birds deserted. In two out of three cases, when I actually captured the bird on the nest before laying, desertion followed.

During laying, there is a marked decrease in the tendency to

desert. Six times I opened tubes with birds inside, and once I forced the mirror into an occupied hole, while laying was in progress but regular incubation probably not started; and no desertions resulted. The one female, however, which I captured and marked during egg laying did desert.

Only three desertions occurred after clutches were apparently complete. In one case (Nest 90) desertion followed my pushing the female off with the mirror and considerably disarranging the contents of the cramped nest. In another (69), when the female was apparently prevented (by obstruction of the passageway) from entering the nest for two or three days after laying was completed, she deserted without beginning to incubate. Nest 74, deserted with incubation about six days along, was disturbed by an unknown party, who had rotated the tube lining so as to dump the eggs out onto the rim of the nest. Though no eggs were broken, I had no way of knowing what mischief might have been done to the adult bird itself. Countless disturbances taking place after incubation had begun seemingly had no effect other than to cause temporary alarm; and in a matter of half an hour to an hour the adult's behavior would again be normal. In the case of Nest 38, desertion did not follow (though the brood ultimately perished) when sand and rocks slid down, a day after hatching was complete, and left the hole only about six inches deep. At least some of the young left Nest 17 successfully, though new excavations had cut the bank back to within a few inches of the nest, probably when the young were two-thirds grown.

Birds were seen intermittently to hover about, perch at the entrance, and even enter briefly, for some hours or even a day or more after a disturbance, although they ultimately deserted. The case of Nest 72 was remarkable in that the female, after being caught and marked, laid one additional egg in the nest the following morning, and then deserted without further disturbance.

Relation to advance of season. The tendency to desert appeared distinctly stronger in late nestings than in early ones, for nine desertions (47.5 per cent) took place in June. Of a total of nine nests which were likely *begun* in June, five were deserted — three of them for no reason evident to me. Thus, of these later nests, 55.9 per cent were deserted, while the 14 desertions among the remaining 89 nestings represented only 15.7 per cent. Some of the late-season desertions — if they can truly be so classified — seem associated with a general weakening of nesting impulses, and correspondingly increased sensitivity to disturbance, once the nesting cycle has been delayed beyond a certain point.

RENESTING

QUESTION OF SECOND BROODS

The Rough-wing, where any statement at all is made, is uniformly referred to as single-brooded. An exception is found in a quotation from Street (*in litt.*, Palmer, 1949: 367-368), in which, however, there is clearly no evidence that two broods were actually raised. It is dangerous to assert that a second brood is *never* reared. However, the complete nesting cycle, from beginning of building to young on the wing, must be considered to occupy an absolute minimum of about 45 days. The earliest broods I have known to leave the nest did so on June 21 (1952), which happens to be also my latest date (in 1950) for the laying of the first egg in a clutch (in Nest 46, which the young presumably left about July 28). Thus the time element alone, as well as every aspect of behavior in the latter part of the season, makes the rearing of a true second brood in Michigan seem virtually impossible. There is nothing in the literature to suggest that behavior is essentially different in regions to the south. Allen and Nice (1952: 630), apparently on Skutch's authority, list *S. r. fulvipennis* as having but one brood a year (cf. Skutch, 1960: 268).

Other species. Double-broodedness among swallows seems to be most characteristic of the Barn Swallow-Cliff Swallow group, the Old World House Martin (*Delichon*), and a few other genera, including the African Rough-wings (*Psolidoprocne*). Allen and Nice (1952: 630) tabulate information from numerous sources, and include data on this point. In North America, the feverish nesting activity of the Barn Swallow throughout the season is a matter of common observation. Most observers "agree that cliff swallows in general raise two broods of young during any one breeding season" (Gross, 1942: 474), although Mayhew (1958: 26) did not find this true in California. The Bank Swallow may be double-brooded here at times (Stoner, 1936: 152, 194-195), and is said to be "as a rule" in Europe (Witherby, *et al.*, 1940: 240). Beyer (1938: 136-137) and Petersen (1955: 251-252), however, found no clearcut evidence of Bank Swallows raising second broods. From my rather incidental three-year observations near Ann Arbor, I would be inclined to agree. Although I have seen very small young as late as July 11 (1950), I have no reason to doubt that they were the result of renestings after first nests had come to grief. Apparently the Violet-green Swallow is seldom double-brooded (Bent, 1942: 379), and the Tree Swallow (Kuerzi, 1941: 26-27; Weydemeyer, 1934: 104) is only exceptionally so; however, Gullion (1947: 412) has found that both these species frequently raise two broods in Oregon. The Purple Martin (Allen and Nice, *op. cit.*: 624-625), despite long-standing misconceptions, apparently raises only a single brood.

SECOND NESTING ATTEMPTS

As distinguished from second broods, second nesting attempts by Rough-wings are common. During 1950 and 1951 I recorded seven clear instances of renesting (see Table 5). The females were marked in two cases, and circumstantial evidence was strong enough in the other five to leave little doubt as to the identity of the birds involved. A number of other late nests probably represent second nestings for one or both parents. Four of the second nestings considered took place in the same holes as the first ones. Three involved moves to nearby holes, the farthest (Nest 88) an estimated 80 yards to the opposite side of Pit "C", but the others a few feet only. In two cases, moves to other holes followed disturbance of the female on the nest, so that desertion likely resulted from fear associated directly with the nest site. In all cases where the same hole was reused, the original nests had been removed, or at least the contents were entirely gone. This latter may not be significant: Brewer (1857: 107) described a case where Rough-wings, near Carlisle, Pennsylvania, had built a second

TABLE 5
KNOWN SECOND NESTING ATTEMPTS AFTER FAILURE OF FIRST
WITH DATA ON BOTH AND APPROXIMATE INTERVALS

First Nest	Clutch of	Incubation Stage	Date Interrupted	Interval in Days	Second Nest	Clutch of	Remarks
66	(One-two days to laying)	May 19	9	88	6	Marked female; hole across pit
72	2-3 (partial)	May 22-23	6-7	87	7	Marked female; doubt as to when deserted. Nearby hole
40	6	1+ days	May 27	9	41	5	Same hole
69	6	*Not begun, 2-3 days	May 25-26	11-12	70	5	Same hole; doubt as to when deserted
73b	6	5+ days	June 4	(10-12) to last building	93	Deserted again, unfinished
86	7	9-13 days	June 7-11	7-11	94	6	Same hole; doubt as to time destroyed
31	6	11+ days	June 6	15	46	5	Nearby hole

* Passageway blocked by toad, after laying.

nest directly on top of a first one, with eggs, that had been spoiled by high water; Skutch (1960: 269) tells of a nest and eggs similarly superimposed upon a deserted clutch in Guatemala.

Four of the second nestings were successful in fledging young; small nestlings were destroyed in two cases; and one second nest (93) was deserted before building was completed. I have never known a third attempt to be made.

Nesting cycle and season. Of the renestings I observed, one (88) followed desertion of a first nest before laying began; one followed desertion during the progress of laying; and five resulted from first nestings being interrupted after laying, or during various stages of incubation. I have no data that suggest any renestings following destruction of young. Rather, in most such cases, the birds shortly disappeared from the vicinity.

Austin (1940: 166) evidently referred to all single-brooded species in his statement that, "for physiological reasons, chick-loss is far less commonly followed by renesting than is egg-loss." Kuerzi (1941: 23-24) recorded one case in which a Tree Swallow renested after a nestling (the first to hatch) was destroyed along with the rest of the clutch of eggs. This species, however, is sometimes double-brooded. Allen and Nice (1952: 625) report that in 1940, when many Purple Martins lost three-fourths-grown young, none of the adults renested. They cite Jacobs (1903: 20), who had a similar experience in 1902, but the next year found (Jacobs, 1909: 41) that many renestings did follow destruction of newly hatched young.

Of the seven second nestings here discussed — I am reckoning now from the *interruption* of the *first* nesting — four (57 per cent) began before the end of May, two more during the first week of June, and the latest (Nest 94) between June 7 and 11. Even in May, I have records of perhaps half a dozen desertions or losses which I have been unable to connect with any subsequent nestings. From June 10 on, there were about 24 nests (over the four-year period) destroyed or abandoned at stages ranging from nest building to nearly time for the young to leave. With one possible exception (Nest 94), I saw no indication that any birds interrupted so late in the season ever tried again. That one known second attempt (Nest 93) never progressed beyond some sporadic building, is in itself suggestive. At least two more nests (42 and 61), partially built in the early or middle part of June, and then deserted for no apparent cause, probably represent abortive second attempts.

Whichever is the essential element, the latest date when initiation of second nesting attempts is to be expected (about June 10) represents roughly the beginning of the hatching period for young of first nestings. By this time regression of the gonads must have proceeded

to the point where it is, for all practical purposes, irreversible. Such authors as Burger (1949) and Marshall (1951), in discussing avian endocrinology and reproductive cycles, give voluminous lists of earlier literature. Stresemann (1927-34: 377) and Laven (1940: 132) give short general descriptions of the progressive shrinking of unused ovarian follicles after laying, which are particularly pertinent here as they apply to the availability of advanced ova for a second laying. Petersen (1955: 267-270) has investigated changes in ovaries and testes of Bank Swallows in relation to their reproductive stages.

Interval before second laying. There is interesting variation in the time required, after interruption of a first nesting, for any new clutch to be produced. Stresemann (*loc. cit.*) and Laven (*loc. cit.*) have correlated this period directly with the lapse of time after completion of the first clutch. Nice (1937: 111) found that the Song Sparrow (*Melospiza melodia*) did not show such correlation, but that replacement sets were almost invariably begun in five days, whether they followed destruction of partial sets, well incubated ones, or nestlings. Kuerzi's (1941: 23-24) findings tended to indicate that the Tree Swallow, while showing considerably more variation than the Song Sparrow, responded in a similar fashion. Both these authors, like Stresemann, point to environmental temperature as another important factor in the replacement time.

In Table 5, the cases of renesting are arranged according to the estimated stages at which the first cycles were interrupted. Some tendency for the corresponding intervals to show a progressive increase is apparent. However, the data are too scanty and inaccurate to indicate clearly the degree of correlation. As the progress of Nest 66 was interrupted before laying, I can only surmise that laying would have begun within a day or so — and here we are dealing with a somewhat different phenomenon. During both longer and shorter intervals occurred spells of inclement weather, none of which were extreme. An estimated average interval might be about ten or eleven days. This is considerably more than the 7.6-day average, for eleven replacement nests, which Kuerzi (1941: 24) obtained for the Tree Swallow; and approximates the ten days which Allen and Nice (1952: 625) report for a single renesting of Purple Martins.

Reduction in clutch size. I have already pointed out that five-egg clutches commonly represent second nestings. Conversely, Nest 94 may be my only bona fide second laying with a six-egg clutch. The first two cases in Table 5 actually represent delayed clutches, and not true second layings.

Allen and Nice (1952: 624) "never found any number other than four" in second sets of the Purple Martin; this represented

a marked reduction. Stoner (1936: 194) found a reduction from "four or five . . . in a first-brood clutch" of the Bank Swallow to "three or four in the second." Kuerzi (1941: 24) found, for his Tree Swallows, that "with only two exceptions . . . the number of eggs in the repeat set equaled the number in the destroyed set." Paynter (1954: 39-41), however, found evidence that clutch size was reduced in second layings of this species. Lack (1947: 309) has pointed out that repeat clutches of some single-brooded species tend to be smaller than the first ones, but that "for birds which regularly raise more than one brood in a season, the problem is in a somewhat different category."

PHYSIOLOGICAL CONTROL OF CLUTCH SIZE

Laven (1940: 132-134) notes that the two capacities for subsequent laying and for continued laying are not easy to delimit. He summarizes experiments by various workers upon a number of species, in which eggs have been removed, usually progressively, during or after laying, with diverse results and sometimes, as in the classic examples of the Flicker (*Colaptes auratus*) and Wryneck (*Jynx torquilla*), with very large total layings resulting.

I was struck by the coincidence of an eight-egg clutch in Nest 23 (1950), completed after two of the earlier eggs had slipped down through the loose lining, and later attempted to determine whether some tactile stimulus might be a factor in limiting clutch size. Three successive eggs were transferred, one each day, from Nest 73 to Nest 74 (1951), during the concurrent laying of the two clutches, starting when 73 held four eggs and 74 held three. Both the resulting clutches were of six eggs, regularly laid; no apparent change of laying or incubation schedule resulted, though one of the artificially produced clutches was of three eggs only (less than any natural clutch I have seen), and the other of nine (more than the maximum recorded for the species). Davis (1955) has reported experiments with Barn Swallows from which he concludes that this bird, like practically all species that have been investigated, is a determinate layer. The results of my single trial indicate that the Rough-wing, also, is no exception.

INCUBATION

The Rough-winged Swallow's incubation seems normally to be carried on exclusively by the female. Although Blake (1907: 104) reported a nesting pair "both taking turns at sitting on the eggs," he indicated that his observations were scattered, and gave no details. Dingle's (1942: 428) statement that "apparently the male occasionally helps his mate with incubation duties," unless based on this single account,

is left unsupported. Birds I have found incubating, or regularly entering holes during incubation, have without exception been identified as females. I saw only a few instances even of the presence of a male in a nest cavity during incubation. His stay was always brief (less than a minute), and in every case *both* birds were in the hole at the time; I have no reason to suppose that such occasional visits play any part in actual incubation. Skutch (1960: 268 ff.) believed that only females of *S. r. fulvipennis* incubated, in the instances observed by him in Central America (cf. Allen and Nice, 1952: 630-631).

It appears (cf. Allen and Nice, pp. 629-631) that, among the swallows of the world that have received special study, the species are about equally divided as to whether or not the male takes a significant part in incubation. The Bank Swallow is one in which the sexes regularly share the duties (cf. Petersen, 1955: 253-255; Moreau and Moreau, 1939a: 95). Although Allen and Nice (p. 629) say the male Barn Swallow assists only "occasionally," others (e.g., Bent, 1942: 448; Smith, 1933: 415, and 1937: 67; Davis, 1937: 70-72; Moreau and Moreau, 1939b: 146-147) have apparently found the habit widespread in that species. Precise information on Cliff Swallow incubation is so scanty that the male's taking part is neither ruled out nor established (cf. Mayhew, 1958: 23). In other North American species active participation of the male is exceptional.

INCUBATION PATCH

Occurrence. Female Rough-wings caught on the nest during incubation have always, in my experience, had very conspicuously developed incubation patches, which males examined have always lacked.

Bailey (1952: 122) states that "incubation patches are found in both males and females according to their participation in incubating the eggs." Elsewhere (p. 127) he reports "never have I found an incubation patch on a male passerine bird." Exceptions to this generality, found in the suborder Tyranni, have been pointed out by Parkes (1953). Bailey suggests (p. 128) that an incubation patch in the male would not be entirely essential for assistance of a sort in keeping the eggs from chilling. That this is true has been clearly shown by Petersen (1955: 254-255) in his study of Bank Swallows. Davis (1937: 70) stated that the brood patch in male Barn Swallows, which he observed frequently incubating, is "not well developed."

Development. Four female Rough-wings I handled before or during the early stages of building (May 10-11) showed little or no evidence of brood-patch development; two with nests partly built (May 3 and May 8), however, were noted as having rudimentary ones. One bird captured early in her laying period (May 22) already had a well-developed brood patch. At least six females caught and examined

during various stages of incubation (May 26-June 29), and seven which had small young (June 14-June 26), all had the patch very strongly developed.

BEGINNING OF INCUBATION

It is of interest to know, as exactly as possible, when the instinct to incubate first becomes effective in the female. Swanberg (1950), in a most enlightening discussion, has pointed out the absolute necessity for clear definition of terms. He cites numerous examples (pp. 67-72) showing that birds can spend extended periods on the eggs without actually incubating. Ryves (1943a: 10) has defined such "brooding" as meaning "to sit on eggs without the production of the requisite temperature to further their development." The same author has repeatedly (*loc. cit.*; 1943b: 42) stressed the frequent confusion of this process with true "incubation," which implies heat production sufficient to advance embryonic development.

The female Rough-wing spends the night in the nest during the laying period; and it appears from my observations that she is generally not only in the nest cavity but actually *on* the eggs. If some of this early sitting is effective, it becomes, as Putnam (1949: 166) concluded for the Cedar Waxwing (*Bombycilla cedrorum*), "impracticable to determine any one definite point at which incubation begins." Not only must "incubation" be distinguished from "brooding," but regular sustained incubation from any preliminary warming, which I am calling *incipient* incubation, that may be effective in the advancement of the embryos. Only combined field and embryological data from many nests, with careful temperature determinations, could fully clarify these concepts. Observations of adults at the nest, and noting whether eggs feel distinctly cool or hot (or neither) have provided me with a basis for tentative judgments. Hatching of eggs in a nest has commonly extended over a considerable period; and from numerous references in the literature, concerning a variety of species, this is generally conceded to indicate incubation beginning before completion of the clutch (cf. Nice, 1937: 122). In the present study, as a matter of fact, the evidence obtained from the sequence of hatching has proved to be particularly enlightening. Discussion of this is reserved for a later section.

Whether or not incipient incubation takes place at night during egg laying, a sustained incubating schedule is initiated by the female near the end of her laying period. This most commonly begins during the day the penultimate egg is laid; less frequently it starts a day earlier, after the laying of the antepenultimate egg, or after the clutch is complete.

Other swallows. Irregularities in the early stages of incubation seem to be the rule among North American swallows. The hatching

time of a clutch of Cliff Swallow eggs sometimes extends over 24, or even more than 48 hours (Stoner, 1945: 208-209); Mayhew, 1958: 24). A pair of Barn Swallows began sitting after laying of the fourth of five eggs, and later after the second of four (Smith, 1933: 415, 419), and hatching was observed to extend over a correspondingly long period. Smith also mentions a day when the eggs were cold for a considerable period, with incubation four days along, the young later hatching normally. Purchon (1948: 151-152) reported gradual daily increases in incubating time of a European Swallow, beginning after the first egg was laid. Petersen (1955: 252-253) found evidence that "incubation [of Bank Swallows] begins with the laying of the third, fourth, or fifth egg." In the case of the Violet-green Swallows, incubation is often commenced before the clutch is complete, and "in one case hatching required five days" (Edson, 1943: 397). Allen and Nice (1952: 625) say of the Purple Martin: "Incubation usually starts on the day the last egg is laid, but since the eggs often hatch on different days, some development must take place earlier." They suggest both the presence of the adults in the nest chamber at night, and the high outside temperatures by day, as factors in advancing embryonic development. Weydemeyer (1934: 103) found the start of Tree Swallows' incubation to range from before the laying of the last one or two eggs to a week after the clutch was complete. Kuerzi (1941: 30) indicates that his Tree Swallows ordinarily did not begin incubation until the first clutch was complete, but that it began sooner with clutches laid later in the season. Austin and Low (1932: 41-42), discussing Tree Swallows, explain (the basis not being made clear) that "development will go on at considerably lower temperatures [than that of regular incubation], but [that] its rate is retarded," and that "cooling in its early stages does not result in the death of the embryo, which will resume its development when it is brooded." They allude to "the small amount of incubation given the first eggs laid while subsequent eggs are being deposited" as a factor in explaining discrepancies in hatching. In the case of the House Martin, Lind (1960: 84-88) attributed wide variation in the observed incubation periods to the often prolonged absences of incubating adults from the nest. Moreau and Moreau (1940: 313) say the African Rough-wing, "*Psolidoprocne holomelaena* . . . has been observed to cover its egg for only 19% of the time on the first day although on subsequent days the percentage varied between about 45 and 60%."

INCUBATION RHYTHM

In my work with the Rough-winged Swallow observation of adults entering and leaving the nest has not been a primary objective, and

my data are accordingly scanty. However, noting the paucity of information on incubation rhythm for the species, I summarize the data I do have, for purposes of general comparison. A total of about 26 $\frac{1}{4}$ hours of observation, made at nine nests during the summers of 1949, 1950, and 1951, seem dependable. Accurately recorded spells spent in or out of the nest tubes by incubating females include 77 attentive and 73 inattentive periods. Times were recorded to about the nearest quarter-minute. Like Moreau (1940: 237) in studies of an African Rough-wing, I have disregarded the time consumed by the birds in going the length of the passageway to and from the nest proper, and timed the birds, on each trip, from the entrance of the tube.

In Table 6 are given the results of some calculations. In the first line are the composite figures for all of the nests observed, data being those gathered at any time during the course of incubation. Lacking adequate consecutive data, I calculated an average percentage period "in" and the average period "out." Three nests provided enough data to justify treating them separately (lines 5-7). While figures obtained from these seem to indicate a considerable variation from nest to nest, more significant changes, I believe, are due to the stage of incubation at which observations were made. I give separate averages for the first two days of incubation, for the last two, and for the remainder of the incubating schedule, combining figures for all nine of the nests used. Data for the beginning of incubation show a higher average for periods "in," and a very much higher one for periods "out"—here incorporated are figures on incubation that has not yet settled down to a normal schedule. In the last stages of incubation (often with one or more of the early eggs already hatching), periods "in" and "out" averaged very short, and schedules were irregular, although the per cent of time on the nest remained comparatively high. Eliminating these records of very early and very late incubation, therefore, gives results (line 3) which may most nearly represent the normal incubation schedule: average spells of 12.48 minutes "in" and 5.08 minutes "out," with the eggs covered for an average of 71.1 per cent of the period of daylight. Skutch (1960: 269-270), from some 6 hours of observation at two nests of *S. r. fulvipennis* in Guatemala, obtained corresponding figures averaging about 58 per cent, with the periods "out" substantially longer.

Nice and Thomas (1948: 146-148) have discussed the relationship between temperature and incubation rhythms; most species studied have shown an increase in percentage of time on the eggs in response to lowered temperature. Skutch (*loc. cit.*) reported such an increase for the Rough-wing. Braey (1946: 162-163) found a correlation for

TABLE 6

INCUBATION RHYTHMS, AS SHOWN BY PERIODS

IN AND OUT OF NEST TUBES AND CALCULATED COVERAGE OF EGGS

Line No.	Nests (of Nine Observed)	Days of Incubation	Total Hours Observation	Periods Used		Periods In (minutes)		Periods Out (minutes)		Per Cent of Time Eggs Covered
				In	Out	Average	Range	Average	Range	
1	All	All	26 1/4	77	73	11.52	1/2 - 38 1/2	5.63	1/4 - 24	67.2
2	All	1-2	5	14	10	13.89	5 1/2 - 36 1/2	10.05	4 1/2 - 24	58.0
3	All	4-14	14 1/2	37	39	12.48	1/2 - 22 1/2	5.08	1/4 - 11	71.1
4	All	15-16	6 3/4	26	24	8.87	1/2 - 38 1/2	4.66	1 - 17 1/2	65.6
5	Nest 11	All	8 1/2	16	18	14.98	2 - 38 1/2	8.76	1 1/4 - 24	63.1
6	Nest 24	All	4	17	14	9.97	3 - 17	4.00	1 - 14	71.4
7	Nest 70	All	9 1/4	27	29	11.55	1/2 - 36 1/2	4.59	1/4 - 10	71.5

the European Swallow, as did Allen and Nice (1952: 626) for the Purple Martin. Moreau (1940: 238-239), however, found no correspondence between temperature and incubation rhythms in the African Rough-wing *Psalidoprocne holomelaena*. From my present data on *S. r. serripennis* in Michigan I am unable to detect any relationship between incubation and weather conditions.

Allen and Nice (*op. cit.*: 631) compile data for several swallow species, on the percentage of time the eggs are covered. My figures for the Rough-wing fall, as would be expected, along with other temperate zone species in which only the female incubates. Tropical species have shown considerably lower percentages (*cf. Skutch, loc. cit.*); and if both parents share the duties of incubation, the resulting percentages are very much higher. In regard to the length of periods "in" and "out," my tentative results do not appear to differ strikingly from those obtained by Allen and Nice (*op. cit.*: 626-628) for the Purple Martin.

BEHAVIOR DURING INCUBATION

Judging from my notes, the commonest basic pattern followed by a Rough-wing pair during incubation is about as follows. The adults return together from feeding, perhaps circle a few times in the vicinity of the hole, and then swoop rapidly up toward it, usually not far apart and with the female in the lead. The female enters for a spell of sitting, and the male veers off at the last instant. He sometimes returns at once to cling at the entrance a moment or two, occasionally entering briefly, or he may continue to circle at a distance. Nearly always he calls, his usual series of quick notes, just as the female goes in. After a period of flying, he goes to his customary perch and adjusts himself for a spell of watching and waiting. When the female again leaves the nest, and flies off to feed, the male generally follows closely, and both disappear from sight. When they return, the process is repeated; and it so continues, with variations, all day long.

Very often the male fails to return with his mate, and comes to his perch alone some time later. He may leave once or twice during the spell of sitting, for more or less extended feeding excursions, and may be absent at the time the female quits the nest. I have no evidence that he habitually "calls her from the nest," as is the case with the male Purple Martin, according to Allen and Nice (1952: 629). Occasionally, however, he will fly to the hole, hover close, possibly enter momentarily, cling, call, or simply circle past the entrance. Usually the female shortly emerges, and the two fly away together. On occasion I have seen a female leave and pass directly over the male's perch, without his making any move to follow; but

he then generally leaves before her return. Sometimes, the female apparently returning ahead of time for a period on the nest, both birds rest on or near the male's customary perch for a few seconds to a minute or more, before the female flies to the burrow. In some cases the male returns alone ahead of the female. He may then simply resume his perch, circle widely about the area and leave, or occasionally investigate the hole by brief hovering or clinging (I never saw one go in under these circumstances). Allen and Nice (*loc. cit.*) say the male Purple Martin "watches the nest" during the absence of the female, and Kuerzi (1941: 27) describes the behavior of the male Tree Swallow, "usually on hand to protect the eggs in the female's absence." The male Rough-wing has, in my experience, demonstrated no such solicitude; his normal behavior is quite the reverse. In studying African Rough-wings, Moreau (1940: 237) found little evidence of the male's coming to the hole, though not uncommonly the two birds appeared together, and later separated, "one entering the hole and the other going on its way."

Position of incubating bird. I had supposed that an incubating female might habitually face towards the entrance of the burrow. It was of interest, therefore, to note that when individuals were seen sitting undisturbed (usually at night), some were facing to my left, some to my right, some directly inward, and some outward. The same bird might be found facing in different directions on successive occasions.

HATCHING

In the nests I studied closely, hatching extended over periods ranging from a few hours to about three and a half days. Van Fleet (1876: 10) mentioned several instances of very wide differences in stage of development of eggs or young in Rough-wing nests he had examined, which (if correct) would imply a wider range of hatching times than any I observed.

Time of day. Skutch (1945: 10) noted that, while birds' eggs might hatch at any hour, the majority seemed to do so during the early forenoon. He quoted Schrantz (1943: 377), who found 110 of 119 Yellow Warbler (*Dendroica petechia aestiva*) eggs hatching at night or in the early morning, and only 9 in the afternoon. Hatching of Rough-wing eggs appears to take place with little or no regard to the time of day. Of 171 eggs hatched, in 30 clutches, about 25 were *known* to have hatched in the morning (4:00 to 12:00 a.m.); about 26 in the afternoon (12:00 to 8:00 p.m.); and 1 during the night (8:00 p.m. to 4:00 a.m.) — this last very low figure due largely to the long periods between my observations. Including the

above, about 35 of the eggs *probably* hatched in the morning, about 42 in the afternoon, and 32 at night. Hatching times of the remaining 62 cannot be assigned with any degree of assurance; but they too appear about evenly divided as to time. It seems probable that with hole-nesting species the temperature and light inside the nest would undergo a minimum of daily fluctuation, and that any differential responses of the hatching young would be correspondingly weakened.

Process of hatching. When eggs hatched normally, the shell broke on a slightly irregular line approximately at right angles to the long axis, and usually a little closer to the larger end than the smaller, so that the empty shell appeared as two fairly regular halves. Braey (1946: 165-166) describes and figures a similar line of cleavage for the eggs of the European Swallow.

On one occasion I was able to follow the progress of hatching of an individual egg, found already pipped, and with a tiny hole in one side. Within 14 minutes the break had been extended three quarters of the way around; in two minutes more the halves were being forced apart, and the young bird was emerging. Another observed instance indicated that hatching is not always so rapid. An egg found pipped at 7:10 p.m. had not changed materially 24 minutes later. By the following morning the nestling was several hours old.

Disposal of shells. Ordinarily I found the shells to have been promptly removed after the hatching of eggs, so that the presence of one or both shell halves in the nest could be taken as an indication of very recent hatching. I found shell halves dropped at varying distances from the nests, along the normal line of flight of the parent birds. Some were immediately below the entrance; but more often they were from 50 to 100 or more feet away. One marked shell half was dropped about 100 yards from the nest. I have no evidence of adults eating any of a shell.

LAYING AND HATCHING TIMES

With data on laying and hatching of the eggs in numerous clutches, in most cases with the eggs individually marked, it has been possible to determine incubation periods with considerable accuracy. In consequence, it has seemed an attractive possibility (using this basic period) to learn more of the pattern of incubation itself, particularly in its early stages.

INCUBATION PERIOD

Swanberg (1950: 75), translating an earlier definition by Heinroth (1922: 173), agreed that "by incubation period is understood the time which with regular, uninterrupted incubation of a newly laid egg

elapses until the young has left the egg.” Nice (1954) has reviewed the frequently misunderstood problem, giving an extensive list of references, and reiterating (p. 173) her earlier support (e.g., Nice, 1953: 81) of the above definition. Figures frequently given, such as those based on total time of *parental* incubation or on the time from the laying of the last egg to the hatching of the first, either depend upon different factors or are quite meaningless. Assuming a proper concept of the term, there are still several variables to be considered in the accurate determination of natural incubation periods (cf. Moreau, 1946; Ryves, 1946).

Existing data. Allen and Nice (1952: 629-631) discuss recorded data on incubation periods of swallows which they consider “dependable,” including figures for a total of 14 species. These figures range from a minimum of 14 to a maximum of 20 days. The authors point out that incubation periods tend to be longer in the Tropics than in the North Temperate Zone, and that hole-nesting species in general tend to have longer periods than open-nesting ones. Four common North American species included have incubation periods given as from 14 to 16 days, that of the Purple Martin ranging higher, from 15 to 17 days (Allen and Nice, *op. cit.*: 625). The most dependable figure for the Cliff Swallow seems to be that of Mayhew (1958: 23-24): 16 days. The period given for the tropical African *Psolidoprocne holomelaena* is about 18 (Moreau and Moreau, 1940: 320) to 19 (Moreau, 1940: 236) days.

Evidently the only authentic incubation-period figures for the Rough-winged Swallow have been those given by Skutch (1945: 21; 1960: 270) for *S. r. fulvipennis* in Costa Rica and Guatemala, where his checks on two nests yielded times of 16 and 18 days respectively. For *S. r. serripennis* there appear to be none. Allen (1938: 85) included the species in a list of common birds for which incubation data were lacking, and I have seen no published response to his inquiry. When Grimes (1930: 5) observed a “full laying” of five eggs, and “exactly two weeks later” found only “one nestling that appeared to be barely a day old,” he at least established a minimum period. Roberts (1932: 44) does not elaborate upon his statement that the “incubation period [is] probably about 14 days”; nor do Sprunt and Chamberlain amplify theirs (1949: 364) that “incubation requires about fourteen days.” Dickey’s figure of 12 days, quoted by Dingle (1942: 428), is obviously too low.

Incubation periods of last eggs of clutches. It seems clear that the most precise method of determining a natural incubation period, based on a minimum of assumption, is that of checking the time (Nice, 1937: 122) “from the laying of the last egg to its hatching.” This presupposes marking of the eggs as laid, and should be exact in

every case where incubation is continuous at least from the laying of the final egg. Then, as pointed out by Nice (1954: 173), "development of the embryo in the last egg continues without the interruptions to which the earlier eggs are subjected."

Figure 4 charts the laying and hatching in 17 nests, in which I marked every egg in the order laid, and fixed within reasonable limits their times of hatching. The narrow ruled columns represent approximately the hours of darkness (assumed for convenience to be from 8:00 p.m. to 4:00 a.m. EST), the wider columns represent the approximately 16 hours of daylight; thus each double column represents a full day. The black ellipses (left) indicate the mornings when eggs were laid, the one open ellipse indicating a degree of uncertainty resulting from a gap in my checking the previous morning. I have aligned the data with reference to the day on which the last egg of each clutch was laid, and the dawn of this day is indicated by the heavy vertical line ("0"). The time in days is read in either direction from this reference line. (While each succeeding *dawn* represents the lapse of a full day, each numbered 24-hour *period* extends from evening — approximately 8:00 p.m. — to evening. This was found most convenient for identifying any given time: thus day "0" is the day the last egg was laid, night "0" the night just before it was laid, and day "—1" the day preceding.)

Solid black triangles represent the observed times of hatching, and wavy lines indicate eggs that failed to hatch. As it was usually impossible to determine the exact moment of hatching, I indicate by the width of *base* of the triangle the period during which each was known to have hatched. (Primarily the period is limited by times of my observations; but in numerous cases I have narrowed the span somewhat on the basis of the appearance of the young when found.) Apexes of triangles usually represent mere guess or assumption, but suggest to some degree a most probable time of hatching.

It is apparent that the several eggs of a clutch, particularly the later ones, tended to hatch in the order of laying. In all of these cases the final egg hatched as late as any other; and in most it hatched from a few hours to a day later. The spread of the hatching times, particularly as correlated with the sequence of laying, can be taken as proof that incubation usually began at some time prior to the deposition of the last egg. It is thus safe to draw conclusions from the hatching times of the 17 last eggs.

In Figure 4, the hatching times of these final eggs fall close to the heavy vertical line that marks the lapse of 16 days from the morning of their deposition. In Figure 5a the same hatching data are plotted to a much larger scale, and in chronological order; the black bars represent the limits within which the respective eggs were known

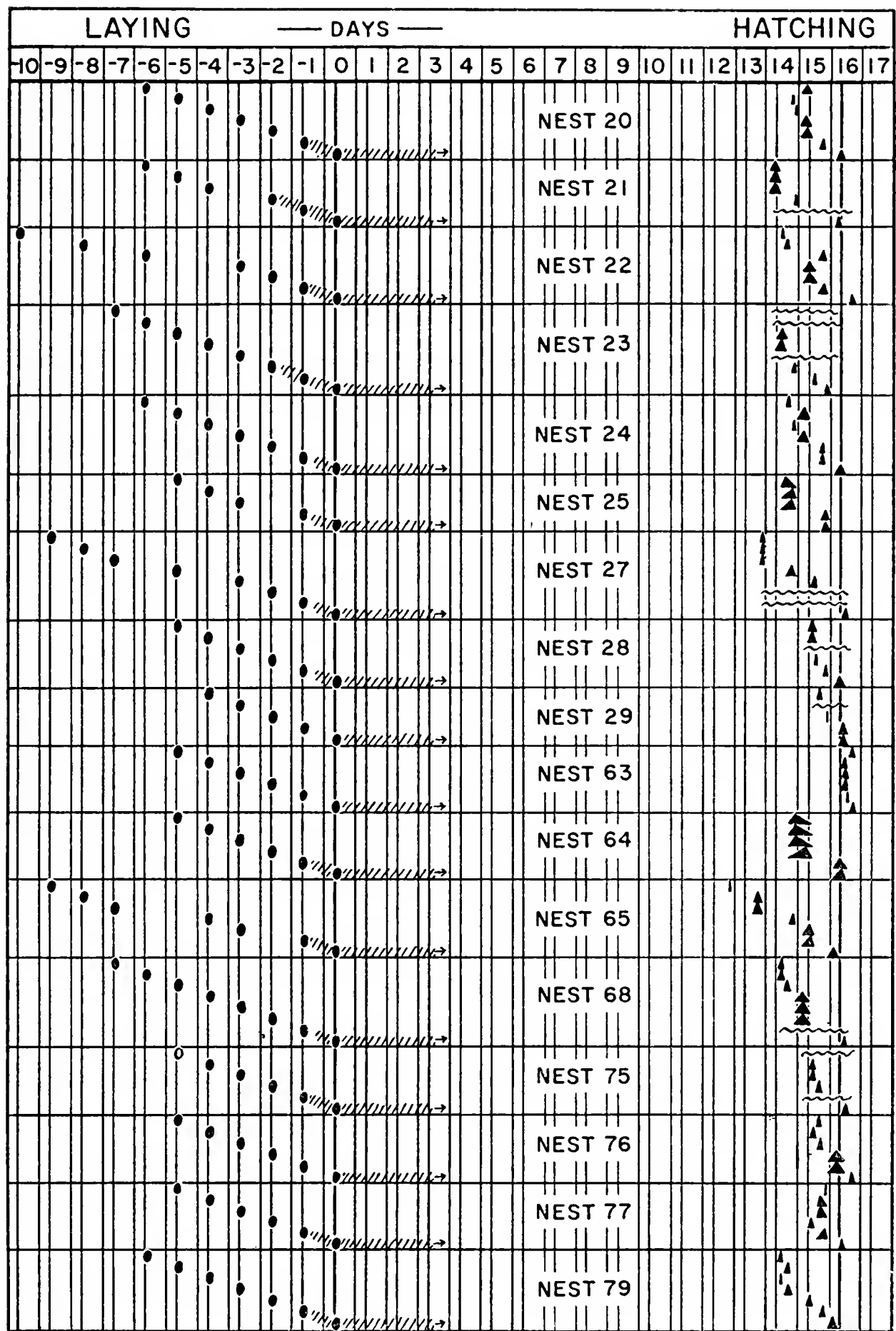


FIGURE 4. Schedule of laying and hatching, as observed in 17 nests with marked eggs. Vertical ellipses mark mornings on which eggs were laid (the single open one denoting possible doubt as to the date of laying); triangles indicate periods during which individual eggs were known to have hatched; shaded bars represent regular incubation inferred to have commenced. Data are aligned, and the days numbered, with reference to the day of laying of the final egg. (For detailed explanation, see text.)

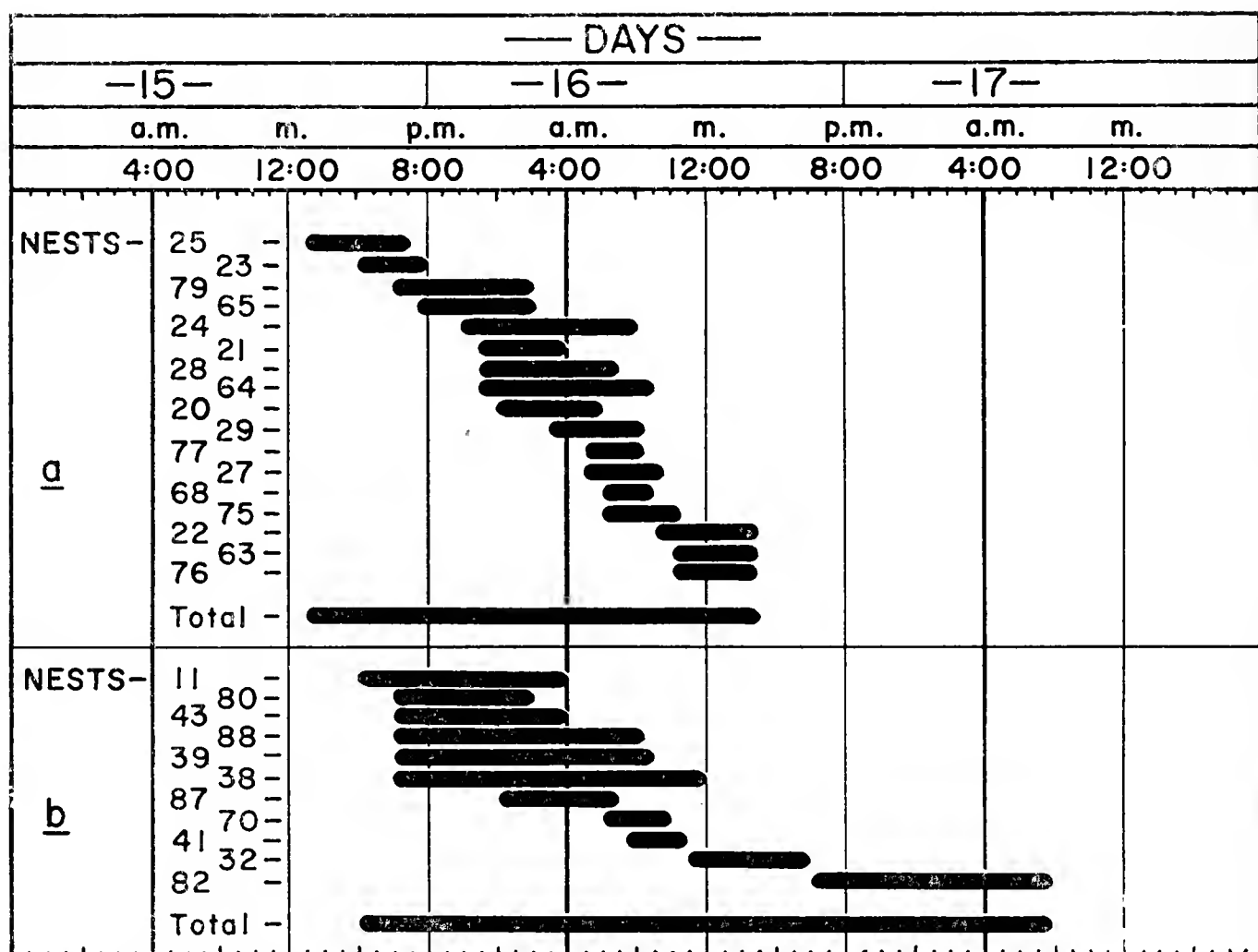


FIGURE 5. Hatching of final eggs in marked (a) and unmarked (b) clutches. In a, black bars represent times during which individual last-laid eggs were known to have hatched (see Figure 4). Days are numbered from the laying of the last egg so that each succeeding dawn (about 4:00 a.m.) marks the end of a full day's incubation. In b, the bars represent known hatching times of last eggs to hatch (see Figure 6).

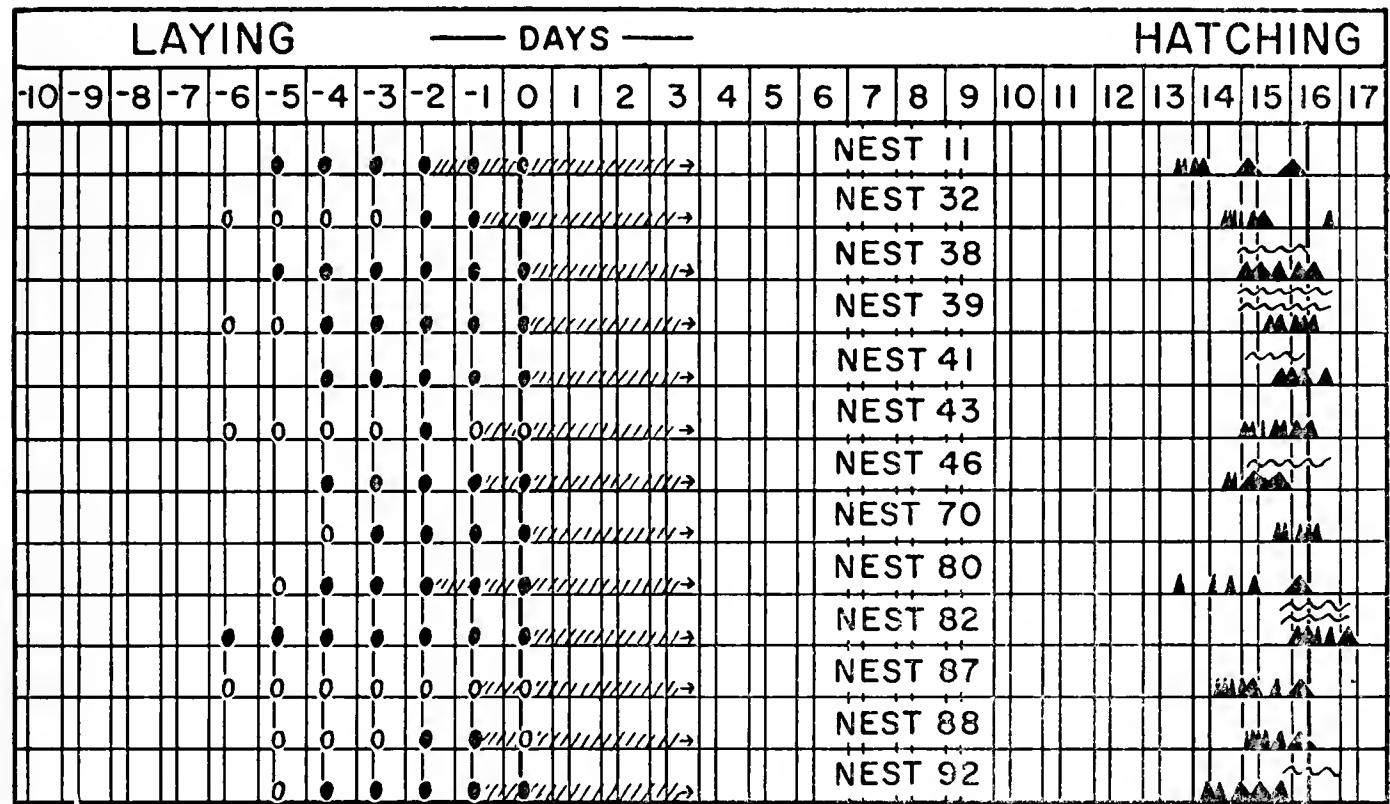
to have hatched, and the left-hand heavy vertical line marks the sixteenth dawn, about 4:00 a.m. If the three latest and the four earliest hatchings are disregarded, the remaining ten lie not over six hours before or six and one-half hours after the 4:00 a.m. line. The total possible range extends from 15 hours before to 11 hours after.

All attempts to apply statistical treatment have seemed to me fallacious because of the margin of uncertainty for each hatching, and the possibility of differences in *laying* time. An incubation period of 16 days seems as precise a one as can be determined from the information at hand. This figure may be an hour or two high, if the eggs are commonly laid some time after daybreak. The diagram itself indicates the range of variation to be expected.

The suppression of some of the earliest and latest hatchings is not entirely gratuitous. In Nests 25, 23, 79, and 65 the last hatchings were most likely not as early as the left end of the bar indicates.

In the first two instances unusually small clutches were being incubated, which is possibly significant (cf. Paynter, 1954: 46-49). In Nest 63 and 76 at least, of those at the late end of the scale, incubation probably did not begin until well after the laying of the last egg; and 22 shows a highly irregular pattern in general.

Figures 6 and 5*b* serve to support the evidence just presented. Laying and hatching times have been plotted about as before for 13 other nests, in which the eggs had not been marked. In Figure 5*b*



Kendeigh, 1932: 143-144). In the large number of other cases in which I had sufficient evidence for a rough check on incubation periods of last eggs, I never found results far from those expected.

Uniformity of incubation period. According to Moreau and Moreau (1940: 313), "there is no doubt that the incubation period is, within narrow limits, specific." From the discussions of such authors as Swanberg (1950), van Someren (1944), and Williamson (1945) it appears that much conflicting evidence is the result of essentially simple factors. Arguments that fundamental differences must exist within successive eggs themselves are not convincing, and according to Swanberg (*op. cit.*: 67-68) no mechanism for this has been demonstrated.

It was clear from Figure 5 that the final eggs showed considerable uniformity, about three-fourths of them hatching within six or eight hours of an average time. For greater deviations some special explanation could frequently be offered. In the complex physiology of the bird's egg (cf. Kendeigh, 1940; Romanoff and Romanoff, 1949: 311-572), many factors are of obvious importance, and much remains to be learned. From published accounts generally (cf. Fautin, 1941: 109-112; Allen and Nice, 1952: 625) it seems very doubtful whether complete uniformity would ever exist for a given species. The suggestion is strong, however, that more and more of the reported disparity will be found only apparent, and that much of the real variation can be correlated with external factors.

It seems fair to assume that *some* factors contributing to variability would be uniform for all eggs in any one clutch. In view of the consistency of my results for final eggs, incubated by different birds, at different times, and in different nests, I cannot presuppose any greater variation among the eggs of a single clutch. It seems to me conservative to consider eight hours as a maximum expected departure from the average true incubation period. Wherever major discrepancies appear, we may fairly seek an explanation first in the details of parental behavior.

PATTERNS OF HATCHING TIMES

Sequence and intervals. Figure 4 does not perfectly bear out the supposition that eggs in a clutch should hatch in the order of their laying. With but one or two exceptions, however (cf. Nests 22 and 64), adjustments much smaller than the expected variation would correct any departure from such a rule. Extremes in the total spread of hatching are found in Nest 63, where all eggs hatched within a single half-day, and in 65, in which hatching extended over about three and one-half days. The remaining nests show variously intermediate situations. This unquestionably reflects variation in the time at which

regular incubation was begun. It appears also to have a bearing upon the effectiveness of any previous warming, during spells the bird may have spent on the nest.

Only scattered accounts in the literature offer anything definite in the way of correlation of hatching times with laying times of successive eggs or with the known start of incubation. Such accounts almost invariably deal with intervals of *days*. In Putnam's study of the Cedar Waxwing (1949: 164-166), it was possible to make continued observations of the female on the nest, and then accurately to fix the hatching times of marked eggs. The observed times of irregular sitting before the end of laying were, to a considerable degree, matched by the intervals between hatching of successive eggs. Evidently the Rough-wing presents a similarly complex problem. Since sufficiently extended nest observations were impracticable, any hypothesis of mine must be based on the premise that intervals between hatchings roughly approximate periods of effective incubation at corresponding times in the laying sequence.

The hatching patterns in Figure 4, and with less confidence those in Figure 6, can be re-examined with this in mind. In each nest there were, in general, initial groups of roughly simultaneous hatchings, which included relatively few eggs, commonly about three (those laid before *any* incubation took place?). The later eggs tended to hatch singly; but except for the final one or two (those laid after *regular* incubation had begun?) they never lagged behind the others by as much as 24 hours. Most of these patterns are best explained by supposing that there was some incipient incubation over a considerable period, before steady incubation began. In fact, satisfactory explanation of the results on any other basis is virtually impossible.

In Figures 7*a* and 7*b* respectively, are the observed hatching times for penultimate and antepenultimate eggs (which hatched) of the several marked sets, plotted together as were those for the final eggs (Figure 5*a*). The long bars below each group represent total hatching spans. In Figure 7*c* these bars are combined with similar ones for the other eggs in the laying sequence, as indicated. As the *end* of laying seems to be the critical time in connection with incubation start, I have numbered the eggs in reverse, the last being "0," the next to the last "—1," and so on. These numbers correspond to the similar ones used to indicate the *days* of laying (Figures 4 and 6) only where an egg was laid regularly every day.

In 7*a* the apparent mean is several hours before the 16-day line. In 7*b* the apparent mean is earlier, but no hatchings are plotted as early as the 14-day line. It is apparent from Figure 7*c* that each bar tends to extend several hours farther to the left than those below, but

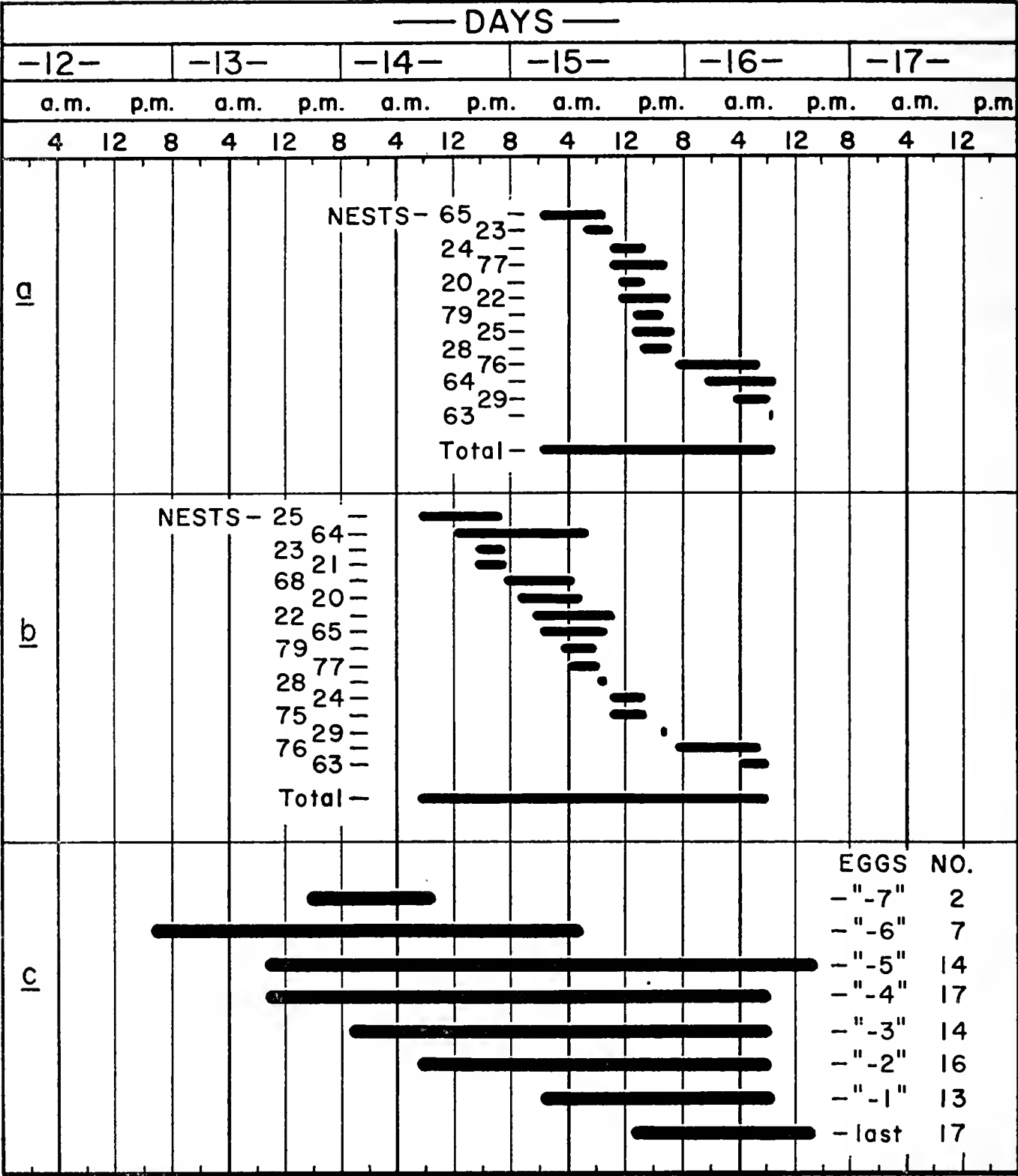


FIGURE 7. Hatching times according to sequence of laying. Bars in *a* represent known hatching times of penultimate eggs in marked clutches (Figure 4). In *b* is shown hatching of the antepenultimate ("—2'") eggs. Days are numbered from laying of last eggs (cf. Figure 5). Periods shown in *c* are totals for eggs in each position, arranged in laying sequence.

never, except for the “—1” and “—2” bars, do the maximum intervals approach a full day. Again, the inference is obvious: that regular incubation seldom began much before the laying of the penultimate egg, and probably never, in the cases studied, until some time after the antepenultimate egg was laid; but that earlier eggs in some clutches had developed somewhat before the start of regular incubation.

Indirect evidence as to start of incubation. The hatching patterns seem to offer the best means available for estimating the start of incubation in any particular nest. Allowing for a moderate individual variation, and for uncertainty in instances where eggs failed to hatch, it is possible to fit each observed hatching pattern to some expected schedule with a remarkable degree of regularity.

Study of the latest hatchings usually suffices to fix the probable starting point of steady incubation, within a half-day or so. Where the pattern is obscured (cf. Nests 27 and 64), there is more uncertainty; but a calculated guess can usually be made.

On Figure 4 I have shown by a shaded band the approximate period of regular incubation that is indicated by the pattern of hatching in each nest. It appears that, of the 17 nestings, there were 2 in which continuous incubation was begun during the day (“—2”) after the laying of the antepenultimate egg; 12 in which it began at some time during the day the next-to-the-last was laid; and 3 in which it did not begin until the clutch was complete. In Figure 6 I have tentatively added similar shaded bands. Although eggs were not marked, the hatching times indicate that the general behavior was similar.

I have supposed it to be the nocturnal sitting that is principally effective in advancing the ultimate hatching of certain eggs, although spells of diurnal sitting may well occur from time to time. That no such process is indicated for *all* clutches, and that *all* eggs in a clutch are seldom differentially affected, removes any likelihood that merely lying for a longer or shorter time in the nest greatly alters the incubation period of an egg. Patterns for Nests 63, 75, and 77 (Figure 4) show no indication of any incipient incubation. In 65 it appears possible that it began after the laying of the first of the seven eggs. It can be judged how many eggs, in most clutches, were included in the initial group of nearly simultaneous hatchings. Their number tends to be inversely proportional to the period by which their hatching was advanced—exactly as might be expected. As a matter of fact, their displacement always approximates one third of the period between the laying of the last (of this initially hatching group) and the supposed start of regular incubation. It is easy to infer that nights of sitting by the female were chiefly responsible. Not

only do hatching times of intermediate eggs support this supposition to a considerable degree; but in certain instances (e.g., Nests 27 and 65) gaps in the laying schedule, matched by corresponding gaps in the hatching, add to the general impression of constant pattern. At the very least, I think it can be said that in some cases there was no incipient incubation; that in most instances there was some, at least during the two or three days (or, more likely, nights) just before constant incubation started, and often from about the laying of the third egg; and that in a few cases some effective warming must have taken place even early in the laying period.

There seems to be little or no relationship between clutch size and the start of continuous incubation. Among the 30 nests upon which I have data there is no evidence of a five-egg clutch having been incubated from day “—2,” nor of incubation of an eight-egg clutch having been delayed until laying was complete. Even these generalities may depend upon the limited sample studied. The extent of incipient incubation seems virtually independent of the commencement of full-scale incubation, of clutch size, and of irregularity in laying.

Correlation with other evidence. I have carefully compared the results of my estimates from the hatching patterns, as regards both steady incubation and incipient incubation at night, with such evidence as I was able to obtain in the field. For about 19 nests I had what I considered a basis for significant comparison. In 11 of these cases there seemed positive agreement; in 6 the evidence was somewhat equivocal; and in only 2 cases did field observations of parental behavior seem to conflict with my deductions from the hatching patterns.

Part IV
LATER STAGES
BROODING OF YOUNG

During their first few days, young Rough-wings are brooded regularly. At first, the rhythm does not differ materially from that of the latter part of incubation, and my records indicate that small young are covered for approximately 60-70 per cent of the time, as are unhatched eggs. In a number of cases I noted unusually long periods of sitting, and extreme reluctance of the female to leave the nest, at and near the time of hatching.

Brooding is carried on primarily by the female, and perhaps by her exclusively, but in some instances the male appears to perform a small part of this duty. The male's spells in the nest with small young always average much shorter than those of the female; and therefore his periods of brooding, if any, are extremely short. Blake (1953: 107), has also commented that the male Rough-wing's feeding visits are very brief.

In Figure 8 are diagrams of some brief records made at nests with small young. In three cases (*b*, *c*, and *d*) unhatched eggs were still in the nest. Shorter and more frequent visits (*a*) reflect the somewhat greater age (2-4 days) of the young. It is seen in *a* and *b* that the males are taking no part, while in *c* and *d* they had already begun their attentions to the young. The pattern in *d* suggests one which I found to be common, and to continue with surprising regularity. After the female had been on the nest for a few minutes the male would enter, presumably with food, and the female would promptly emerge and fly off. The male would remain, but from a few seconds to a minute or so afterward would also leave, to re-enter at the end of the female's next spell of brooding.

DURATION OF BROODING

Diurnal brooding seems to cease about five days after the earliest hatching. I always found evidence of its continuing regularly in nests with young less than four days old. My records all show that little or no brooding occurred with young older than six days.

The female continues to remain on the nest for about three or four nights after diurnal brooding has ceased. My records of this are

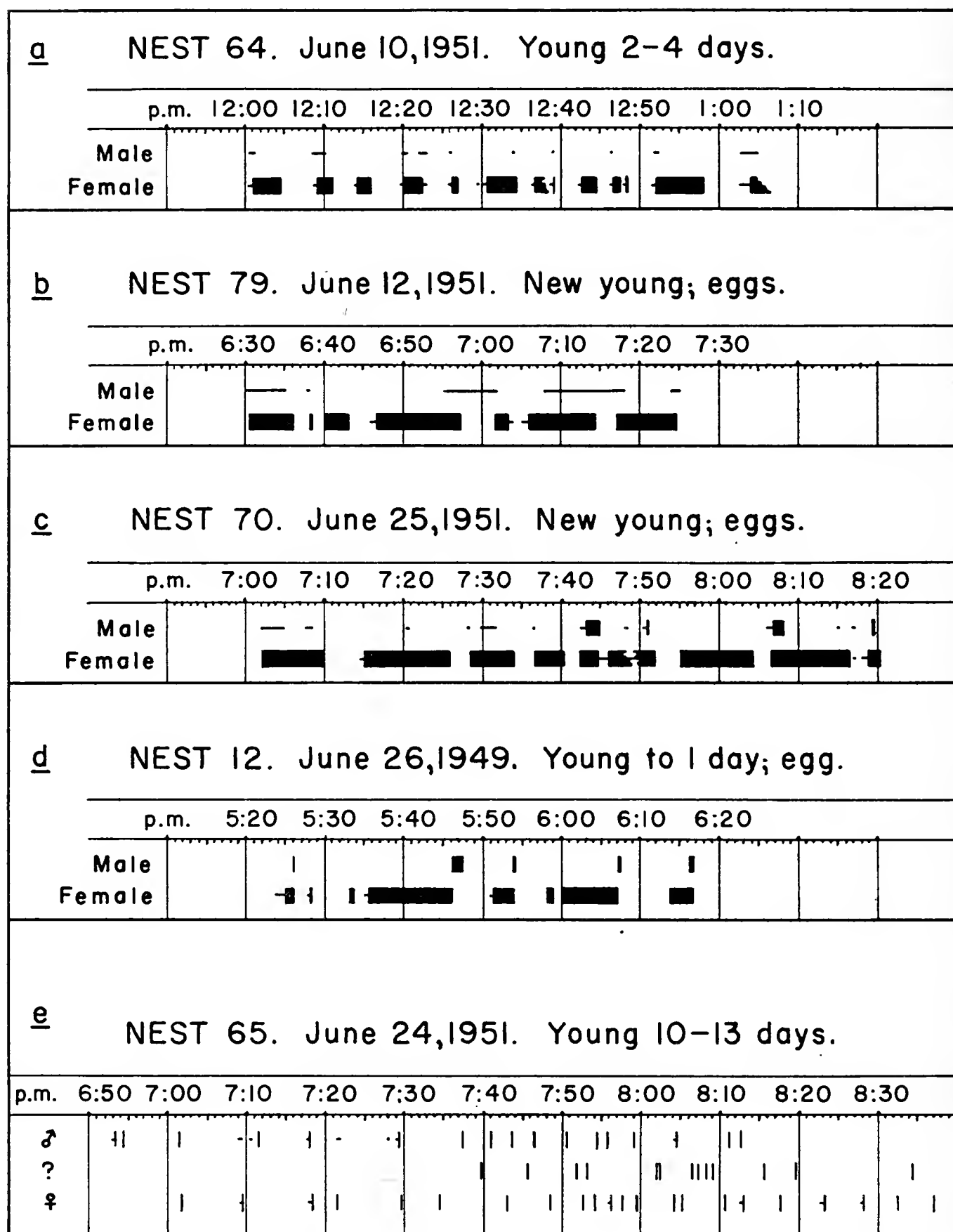


FIGURE 8. Sample brooding and feeding rhythms. In *e* are indicated feeding trips by both parents, with greatly increased rate just before dusk (frequently, in the failing light, the bird was unidentifiable). Broad bars, and vertical lines, indicate time in nest tube; thin horizontal lines denote a bird in sight, perched or circling near nest.

based on seven nests, all in 1951, in which I found females roosting with young 1 to 3, 6 to 7, and 7 to 8 days old. Young 7 to 9, 11 to 13, 16 to 17, and 17 to 19 days old were unattended at night. Thus the female has not been found to spend the night in the nest after the oldest young have reached an age of about nine days. The data I have thus far are entirely consistent.

Interpretations. The cessation of parental brooding could act as an adverse factor in the development of the smallest young, in broods with a wider-than-average range in age. In my studies, however, I have found no evidence of any detrimental effects. I have made no studies of body temperature and so cannot correlate its stabilization in the young exactly with the end of brooding. Stoner, in studies of Bank Swallows (1936: 179-180), Barn Swallows (1935: 407), and Cliff Swallows (1945: 210, 215), found extreme fluctuations in the body temperature of nestlings for the first few days, with stabilization taking place by about the 10th day in the latter two species. Dawson and Evans (1960) report investigations on the development of homeothermy in Vesper Sparrows (*Pooecetes gramineus*); they briefly summarize (p. 337) data for several passerine and non-passerine species, and conclude that "the speed with which homeothermy is established thus appears to correlate with the general pattern of development." The 6 to 7 days required for Vesper Sparrow nestlings to develop effective temperature regulation, as compared to 9 or 10 days for swallows, is consistent with the shorter fledging period of the former. But by the time parental brooding ceases, young Rough-wings would not be expected to suffer from the ordinary fluctuations of temperature in sheltered nests.

BROODING HABITS OF OTHER SWALLOWS

It appears that brooding behavior comparable to that of the Rough-wing is characteristic of swallows in general. Studies of the Purple Martin (Allen and Nice, 1952: 634), European Swallow and Barn Swallow (Owen, 1918: 226; Davis, 1937: 71), Bank Swallow (Stoner, 1936: 195; Beyer, 1938: 128-129, 135), Cliff Swallow (Viator and Viator, 1912: 150), Violet-green Swallow (Edson, 1943: 398), Tree Swallow (Austin and Low, 1932: 42; Kuerzi, 1941: 30), Wire-tailed Swallow (*Hirundo smithii*) (Moreau, 1939: 116-119), and the African Rough-wing *Psalidoprocne holomelaena* (Moreau, 1940: 242-243) tend to show that the young are brooded for a few days only, and about as much as the eggs. Where the male had helped to incubate, he participated actively in brooding as well. Young Blue-and-White Swallows (*Notiochelidon cyanoleuca*) (Skutch, 1952: 400) were evidently brooded for about two weeks. Presumably, in species that normally roost in holes or under cover, as the Bank Swallow,

Barn Swallow, Cliff Swallow, and Blue-and-White Swallow (cf. Skutch, *loc. cit.*), one or both parents often spend the night on the nest well beyond the period of actual brooding.

ROOSTING

ROOSTING IN THE NEST CAVITY

According to Howell (1924: 268), Rough-wings in Alabama "are said to gather [in autumn] into large flocks and to roost at night in their burrows." This report, I think, is almost surely unfounded. Blake's observations (1953: 107) in Massachusetts "suggest that the male does not roost in the burrow even after the eggs have hatched." In my experience, the male very seldom, if ever, spends a night in the nest hole, and the female ordinarily does so only during her laying, incubation, and brooding. Skutch (1960: 270) found only incubating females sleeping in burrows in Costa Rica.

I have made numerous spot checks with a light, on a total of 12 nights during the seasons of 1949-51, which collectively gave a good coverage of all stages of nesting. Most roosting Rough-wings observed on these occasions moved so as to face the entrance, many advanced a short distance toward me, and some actually flew out during my presence near the nest. On the other hand, certain birds, particularly during the early morning hours, seemed so oblivious to the light on them that I was able to observe them sleeping undisturbed, often with bill tucked under the scapular feathers. The evidence invariably pointed to their being females.

Early in my study I had assumed that the Rough-wings would habitually roost in the burrows. Therefore I made careful night inspections of all available holes, from about the time of the birds' arrival (with the particular aim of capturing and marking some at the beginning of the season). It was soon apparent, however, that they were generally not to be found thus until laying began. I could count on finding Bank Swallows roosting in any holes deep enough to provide shelter; and two were usually present in each burrow. But with two exceptions (both on May 11, 1951: Nests 19 and 31), cavities known to have been claimed by Rough-wings were unoccupied — save that in one or two cases a Bank Swallow was found roosting on a partially built Rough-wing nest.

General tendencies of swallows. I think that hole-nesting swallows are commonly assumed to roost in the cavities more regularly than actual observations indicate. Even Bank Swallows (Beyer, 1938: 136) "leave their young alone in the burrows at night after they are partly grown, the adults flying away to roost with others of their kind in a marsh." Smith (1937: 67) reports that five days

before the departure of a brood of Barn Swallows (which do not, of course, nest in holes) he "verified the absence of the female from the nest and the absence of both parents from the shed." He further stated: "Where they spent the hours of darkness . . . is a mystery."

Blue-and-White Swallows (Skutch, 1952: 397) and Black-capped Swallows (*Notiochelidon pileata* — Skutch, 1960: 277-278) sleep in burrows even when not nesting. In the case of Cliff Swallows (Viator and Viator, 1912: 150) and Purple Martins (Allen and Nice, 1952: 618-619), roosting in the nest chamber is the usual thing during a considerable part of the nesting season. However, both Allen and Nice (pp. 617, 634) and Widmann (1922: 11-16) allude to Martins roosting elsewhere than in the house both before and after nesting. For the Violet-green Swallow in Washington, Edson (1943: 397-398) reported that "often the birds hole up in the box for the night before eggs are laid," and that "occasionally one bird spends the night on top of the box while the other is inside." According to Kuerzi (1941: 10) Tree Swallows "in the pre-egg-laying period . . . are absent from the boxes no matter what the climatic conditions." Weydemeyer (1934: 101) writes: "Just where the nights are spent by the female [Tree] Swallows during this time [soon after arrival], and by the male birds throughout the season, still is to me a mystery. . . . Two to six weeks after their arrival . . . the female Swallows begin staying in their houses at night. After egg laying commences, they remain on their nests at night regularly. . . . As a rule, at no time during the entire season do the males share the houses at night." Thus the reported Tree Swallow behavior, in particular, is quite reminiscent of that of the Rough-wing.

ROOSTING IN OTHER LOCATIONS

If the Rough-wings did not ordinarily roost in the holes, except to the extent that breeding activities made it necessary for the female to do so, I was eager to discover where they did spend the night. My information is still only fragmentary. I observed the general movements as dusk was falling, and always found some Rough-wings still flying until it was too dark to follow their courses clearly, and heard individuals calling after I could no longer see them. Those feeding young remained active as long as there was any light. By watching nest entrances, I could often see incubating or brooding females enter the holes, apparently to remain for the night; but the rest of the birds disappeared without giving a clue. Males have appeared in the vicinity of the nest with the first light, when the female is laying or incubating, and have, to all appearances, come from a considerable distance. When I observed a brood of recently fledged young apparently preparing to go to roost

along a bushy fence row, the female (?) parent appeared to have been with them or close by.

My most significant observations were made the evening of June 26, 1951. Watching swallows until dark in Pit "B", I became aware of a general movement toward a small marshy pond to the north (see map, Figure 1), which seemed to involve a few Barn and Bank Swallows, as well as most of the Rough-wings. It appeared that the majority, if not all, of the individuals finally remained in the vicinity of the pond. From the frequent calls, I concluded that most Rough-wings observed were males. One was a marked female whose nest (88) had been found destroyed about three days before. I saw several birds actually alighting in small willows and aspens, and lower, in the cat-tails. Others flitted about seeking perches, mostly back in the edge of the willows; and a few were still circling until I could no longer see. On June 11, 1952, I watched again at the same location. Although I noted a definite movement of both Rough-wings and Barn Swallows in the direction of the pond and the surrounding marshy area, I was unable to establish whether any were actually going to roost there, as on the previous occasion.

Summer roosts. Late-summer and autumn swallow flocks are a familiar sight in the marshes, long ago vividly described by such writers as Chapman (1900: 95-105), Bartsch (1898: 64), Sawyer (1918), Widmann (1899), and others. Henshaw's account (1875: 219), quoted in part by Dingle (1942: 430), does not make clear at what season he observed very large flocks of Rough-winged Swallows roosting in dead bushes along the Provo River in Utah.

Despite repeated reference to the build-up of flocks through the summer months, the question of the composition of the earlier roosting aggregations seems largely to have been overlooked. Fisher described summer roosts he observed at Sing Sing on the Hudson. Barn and Bank Swallows were identified, but (1896: 384) "whether the eave [= Cliff] swallow or rough-winged swallow occurred at all was not determined. . . . During the summer of 1885 . . . all the specimens collected [going to roost] were adult males."

By "summer roosts" Fisher (p. 382) "meant such as are occupied by the old males, while the females are still sitting on the eggs and before the young have left the nest." He suggested that such roosts were probably common, though undetected. That they are important in the behavior of the Rough-wing, at least, seems strongly indicated by my observations. Considering what I have been able to learn in the gravel pits, I feel confident that most of the roosting Rough-wings are to be sought elsewhere. It is reasonable to infer that groups of males gather nightly throughout most of the season, and that they are joined by females not remaining on nests, and quite possibly toward the last by groups of newly fledged young.

FEEDING AND FOOD OF NESTLINGS

ROLES OF THE SEXES

Both sexes of the Rough-winged Swallow share in feeding the nestlings. I have never found an exception to this, although Blake (1947), observing a Massachusetts nest, found that "the male rough-wing seemed to take rather little part in feeding the young." Blake (1907: 104) reported that at a nest in Vermont "both were feeding young." In some instances the male begins making trips to the nest (and presumably carrying food) very shortly after the young have hatched; in others it may be at least three days before he takes any part in the feeding. In any event, the male's solicitude increases, until by the time the young are a few days old both parents are making trips with about equal frequency.

Moreau (1940: 237) says that "in *Psalidoprocne [holomelaena?]* . . . there is practically no evidence that both birds share either incubation or feeding." Otherwise, in all Hirundinidae for which data are readily available, both sexes have been found to feed the young.

TABLE 7

SAMPLE FEEDING RHYTHMS, AS OBSERVED AT NESTS
WITH YOUNG OF VARIOUS AGES

Age of Young in Days	Number of Young	Nest Number	Length of Observation (minutes)	Proportion of Trips by Male	Proportion of Trips by Female	Total Trips	Approximate Average Interval
4-5	4	12	45	33%	67%	15	3 min.
3-6	7	65	75	59%	41%	22	3.4 min.
6-7	4	12	45	54%	46%	13	3.5 min.
7-9	6	79	70	50%	50%	28	2.5 min.
10-12	6	79	60	80%	20%	25	2.4 min.
10-13	6	65	110	44% ^a	56% ^a	52	2.1 min.
14-17	6	65	25	100%	None	2	12.5 min.
17-19	3-2 ^b	79	90	60%	40%	5	18 min.

^a Of trips where parent was identified. For 25% of the total observed visits, the sex was in doubt because of poor visibility. The male, being unmarked, probably was responsible for the majority of these.

^b As young were in the process of leaving the nest.

Decline in female's attentiveness. In Table 7, I have summarized the results of observations (a total of about $8\frac{2}{3}$ hours, at three nests), where the females had been marked, and where I was able to obtain reasonably complete records of feeding trips, complicated by little or no brooding. Both parents shared about equally in the carrying of food, until the young were about two-thirds grown. Then there was an appreciable drop in the female's activity, relative to that of the male. In Nest 65, when the young ranged up to 13 days old, the female probably was still making about half of the observed trips; but four days later she was not seen at all during the hour I watched.

The significance of this drop in the female's attentiveness is not clear, and I have not seen similar behavior described for other swallows.

FREQUENCY OF FEEDING

Changes during growth of young. Table 7 shows that the frequency of feeding at first increased from about one visit every 3 to 3.5 minutes (a rate of about 17-20 per hour) to almost one every 2 minutes (30 per hour), as the age of the young increased. The rate then dropped sharply again, as the end of the nestling period approached. Though the attentiveness of the female first began to decline, that of the male shortly did likewise. The bottom two lines show feeding at the rate of only one visit every 12.5 and 18 minutes (4.8 and 3.3 visits per hour) respectively. (In the final case one of the brood had left the nest when my observations began, and one more left shortly.) This reduced feeding rate may well be a factor in stimulating the young to leave the nest, as suggested for irregular behavior at the nest of a European Swallow by Moreau and Moreau (1939b: 150).

Rates, and factors influencing them. Comparative data (some of them far more extensive than mine) are available for a few other swallow species; they show feeding rates both higher and lower than those I have observed for the Rough-wing. Braey's (1946: 177) observed feeding rates for the European Swallow ranged from a minimum of 3 visits an hour (during a rain) to a maximum of 73; this author provides detailed records, and correlates the feeding rates (pp. 170-176) in part with changes in weather conditions. Both Davis (1937: 71) and Wood (1937a: 32) have commented upon very irregular feedings by Barn Swallows. Moreau (1940: 243-245) gives a good analysis of the very slow feeding rates observed for an African Rough-wing (*Psalidoprocne holomelaena*), where for one nest most of the intervals between feeds were 8 to 15 minutes, and for *Hirundo smithii* (1939: 123) shows that "the peak of the frequency curve is at 2-3 minutes" for intervals between feedings.

I have no data adequate for determining the relation of feeding frequency to brood size. Allen and Nice (1952: 635), in discussing data on Purple Martins, consider it "evident that both age and number of young influence the rate of feeding." In other swallow studies (e.g., Moreau, 1940: 243-244; Moreau and Moreau, 1939a: 96), it has been pointed out that feeding rates and brood size are not necessarily correlated. Most observers have found that ordinarily only one of a brood of young swallows is fed at each visit by a parent (cf. Owen, 1918: 227; Beyer, 1938: 129); but Moreau (1939: 123) states that, in a brood of two young of *Hirundo smithii*, both were fed at nearly every visit for the first 4 days, and only one after 8 days. In my Table 7 the maximum rates indicated for a brood of 6 (an average brood for the Rough-wing in Michigan) might approach 5 feedings per hour per nestling.

I have little evidence of diurnal rhythm in the feeding behavior of the Rough-wing. Figure 8e shows graphically, however, the marked acceleration of feeding at one nest as dusk approached. From 7:50 to 8:10, the rate is seen to average exactly one visit a minute, although in the failing light I could not always be sure which parent was entering. My other observations indicate that this stepped-up schedule is a universal feature of the feeding behavior. All the young were presumably crammed to capacity with food before the parents departed for the night.

DURATION OF FEEDING VISITS

The length of visits generally decreases as the young get older. The average estimated time at the nest was about 10 to 15 seconds when young were 3 to 6 days old, and only about 6 or 7 seconds when they were half grown. When nearly fledged, the young often come forward into the passageway, and the adults leave even more promptly (often after only 2-3 seconds); at this time the parent frequently has to *back* out of the entrance (if it is narrow), as is rarely the case when young are smaller. Longer visits are sometimes, but not always, associated with the removal of fecal sacs. The female, in general, remains longer in the nest than the male. Occasionally, when the young are as much as 10 or 12 days old, a female will spend a period of a minute or two in the nest, even remaining while the male makes one or two visits. The significance of this is not clear. Regularly, I have known both adults to be in the nest cavity at the same time when feeding young. Toward the end of the fledging period, however, when there is very little space for movement in most nests, one often waits, hovering or circling briefly, until the other emerges.

FOOD

In a nest with young up to about 11½ days old, I found a small, black, winged hymenopteran (unidentified) sticking to the corner of the mouth of one nestling. In a nest with 2- to 4-day-old young, I found a yellow and black syrphid fly, dead, and about 10 mm. long. Both parents of Nest 60 were collected, when the young were an estimated 3 to 4 days old, with mouths crammed with insects; from a superficial examination, these appeared to be mostly an assortment of medium-sized, stout-bodied Diptera. At least one parent feeding 6- to 8-day-old young had very long, pale appendages protruding from its mouth in all directions, as if the food consisted mostly of Tipulidae (Crane-flies), or possibly of Ephemera (May-flies). After the young had flown from one nest, I noted the remains of four syrphid (?) flies, yellow and black, and about ½ inch long.

These observations do not altogether correspond to those of Widmann, who reported (1922: 9) that the age of Purple Martin nestlings can be judged "from the size of the insect which the parents bring." It appears that assorted soft-bodied Diptera may provide a large proportion of the food of young Rough-wings during all of their period in the nest — insects that have been shown to be predominant in the over-all diet of the species.

NEST SANITATION

I have repeatedly seen adults of both sexes carrying out fecal material after feeding, but females probably do a somewhat larger share of the nest cleaning. The only published comment I have seen is an account by Lewis (1944: 15) of Rough-wings he watched along a canal near Ottawa, Ont., carrying out fecal sacs and dropping them into the water. Information on other species of Hirundinidae indicates that, in general, both sexes assist. Kuerzi (1941: 32) stated that in the case of Tree Swallows the sacs "were carried from the nests mostly by the females." Edson (1943: 400) states that the Violet-green Swallow "nest is kept wholly clean while the nestlings are small, but [that] after their eyes are open the surroundings become progressively foul."

Disposal of fecal pellets. With some species, at least, pellets are swallowed during the nestlings' first few days, and later carried from the nest (cf. Beyer, 1938: 129-130; Davis, 1937: 71; Owen, 1918: 226). This is possibly true for the Rough-wing. I have noted adults carrying out pellets when young were 3 to 6 days old; but have only one doubtful record of a female carrying one from young hatched only a few hours. However, the fecal sacs of such small young would seldom be visible in the parent's bill as it left the hole (cf. Moreau, 1940: 242).

The adults generally carry the pellets a considerable distance; I have seen pellets dropped at 100 to 200 feet from the nest, and in numerous cases the birds seemed to be still carrying the material when I lost sight of them. Kuerzi (1941: 32) reports Tree Swallows that “transported the sacs some 700 feet” to drop them in the water, and calls attention to Stoner’s (1936: 196) similar report for the Bank Swallow. The Rough-wings I observed often did drop sacs into the water; but whether this was more than coincidental I cannot say (cf. Lewis, *loc. cit.*).

Bank Swallows (Stoner, *loc. cit.*) and African Rough-wings (Moreau, 1940: 241-242), when large enough, move so as to defecate clear of the nest pad, though still within the tunnel, where the excrement is gathered and removed by the parents. Apparently, young Rough-wings, after a time, deposit their excrement over the edge of the nest proper. There is variation in the thoroughness with which the adults then keep it removed. After young are 10 to 12 days old, it becomes increasingly common to find fecal sacs neglected on the nest rim or along the passageway. In some cases the nests became quite stained with droppings by the time the young had flown; but in other instances most of the feces were removed until the last. I saw one female leave with a fecal sac half an hour before the last two fledglings flew from the nest.

Notes on fecal sacs. In the process of weighing large numbers of nestling Rough-wings, I had occasion from time to time to examine fecal sacs of birds that defecated during handling. Pellets of very small nestlings, up to perhaps 3 days, appear comparatively dry and slender. Those of newly hatched young have failed to register any weight on my platform balance, and therefore must weight considerably less than 0.1 gram. As young develop, their feces are in the

TABLE 8
RELATIVE WEIGHTS OF SOME SAMPLE FECAL SACS

Nest Number	Date	Weight of Young	Weight of Fecal Sac	Approximate Per Cent
24	June 18, 1950	11.2 gm.	0.4 gm.	3 1/2
23	June 22, 1950	12.6 gm.	0.3 gm.	2 1/2
24	June 18, 1950	15.0 gm.	0.5 gm.	3 1/2
12	July 4, 1949	17.7 gm.	0.75 gm.	4
21	June 22, 1950	(17.1-19 gm.)	0.7 gm.	4 ±

form of typical fecal "sacs," with much liquid, and encased in a resistant mucous envelope. In Table 8 I have summarized a few incidental weight data. The samples, though voided during the excitement of handling, were never obviously abnormal, as was the semi-liquid excrement Stoner (1936: 196) describes as voided by young Bank Swallows while held. It is apparent that for a time single sacs represent up to at least 3½ to 4 per cent of the weight of the young birds. The droppings of young of 18 to 20 days tend to be smaller and less liquid, to be losing their definite form as "sacs," and to approach the appearance of adult excrement. These changes (more or less common to all young passerines, at least) are to be expected, in view of the changes in the feeding and growth of the nestlings. However, they could, to a great extent, account for changes in parental behavior, so far as nest sanitation is concerned.

GROWTH AND DEVELOPMENT OF YOUNG

It has been shown that swallows as a group have a rather characteristic pattern of nestling growth. On account of the birds' peculiar mode of feeding, the period in the nest is of necessity unusually long. When finally ready to quit the nest, young swallows are physically well advanced, and the subsequent period of parental care is brief. Particularly useful accounts of nestling development are to be found in the work of Stoner (1936: 158, 177-178), Beyer (1938: 127-136), and Petersen (1955: 263-264), on Bank Swallows; Braey (1946: 187-191) on European Swallows; Stoner (1935: 402-407) on Barn Swallows and (1945: 209-216) on Cliff Swallows; Low (1933: 80-85) and Paynter (1954: 103-110) on Tree Swallows; Edson (1943: 399-402) on Violet-green Swallows; and Allen and Nice (1952: 632-635) on Purple Martins.

Among my field notes are comments relevant to the growth of at least 44 separate Rough-wing broods, and a number of additional nests with young were casually observed. Thus my generalizations are often based upon considerably larger samples than figures pertaining to specific analyses would indicate. Since hatching may occur at any time of day or night, and members of a single brood differ considerably in age, I have endeavored to minimize the resulting ambiguity. In some instances I am able to give ages to the nearest half-day; in others they are known only to the nearest day, or the half-day intervals are disregarded for purposes of clarity or convenience. But in all cases I refer to the nearest actual age of the *individual* from its time of hatching.

PLUMAGE

Nestlings of known age, from a number of different nests, were preserved as alcoholic specimens, or in a few cases as study skins. Some of them represent, as shown in Plates II and III, a developmental series covering, at intervals of about one day, the time from hatching to nearly full development of the juvenal plumage. Variation between individuals and between broods is found to be of such an order that average conditions can be quite safely described, and the figured specimens shown to be reasonably typical of their age groups. As a guide, particularly in terminology, the very detailed study of House Wren (*Troglodytes aëdon*) ptilosis by Boulton (1927) has been especially useful.

Natal down. Newly hatched young Rough-wings appear quite naked. The sparse down is soaked and dark, and therefore scarcely visible, for the first two hours or more. The bodies are at first bright pink, more yellowish on the abdomen, "with the blood vessels and organs showing somewhat through their skins" (Dingle, 1942: 428-429). Within about 4 hours, usually, the down has begun to dry, but it is generally 9 to 10 hours or more before all the down feathers are fully fluffed out to the tips. Within the first day or two, the skin tones become slightly less yellowish ventrally, and somewhat paler pink elsewhere, probably as a result of the drying and hardening of the outer epidermal layers.

The natal down is very pale gray. I have examined ten alcoholic specimens, all carefully collected and handled, and none older than 3 days, and found the number of neossoptiles to range from 29 to 40 (average, 33.7). In the paired superciliary rows I found on the left from 2 to 6 (3.7) feathers and on the right from 2 to 5 (3.3); in 60 per cent of the sample these were asymmetrical in number. The roughly transverse occipital row, or group, had from 4 to 8 (5.4) down feathers. In the dorsal spinal tract, paired rows extend forward from above the hip joint to converge near the middle of the back; I have counted from 3 to 6 (4.4) feathers on the left, and from 3 to 6 (4.6) on the right, the number being asymmetrical in only 20 per cent of the sample. The humeral tracts had from 5 to 7 feathers, averaging 5.9 on the left and 6.1 on the right, asymmetrical in 60 per cent of the specimens. In a single individual I noted 3 additional neossoptiles: 1 in the center of the lower back between the two longitudinal rows, and 1 in each femoral tract just posterior to the thigh.

Minute hooked filaments are visible where the tips of the rectrices are to appear. These are present at hatching, but later elongate very slightly, to something over half a millimeter. Boulton (1927: 401) is inclined to regard such filaments in the newly hatched House Wren

as degenerate neossoptiles. In the Rough-wing I have detected no such filaments representing the remiges until about the third day, when the primary sheaths are appearing close to the surface — this despite the fact that the primaries actually erupt before the rectrices. Thus, in the caudal tract, the filaments seem indeed to be more than “merely the attenuated tip of the forthcoming feather sheath” (Boulton, *loc. cit.*).

The natal down varies among species of swallows. In the Bank Swallow it is gray (Beyer, 1938: 127). In the Barn Swallow it is “smoke-gray” (Dwight, 1900: 227). Edson refers to “creamy” down in both Tree Swallows (1939: 12) and Violet-greens (1943: 399). In Purple Martins, according to Allen and Nice (1952: 632), the down was gray when present, but most young observed were “entirely devoid of natal down.”

Acquisition of juvenal plumage. By the end of the first day dark areas, in the wings of young examined in the field, mark the appearance of the developing remiges beneath the skin. The dark area is heaviest, and appears first, in the region of the middle primaries, and spreads distally and proximally.

In young 2 days old, the dark line of secondaries is becoming evident along at least the distal portion of the forearm, and a faint dark crescent usually indicates the location of the incoming rectrices. In some individuals the spinal tract may be just discernible as an additional dark area, most prominent near the middle of the back.

After 3 days the average young have the spinal tracts distinctly visible; the regions of the capital, humeral, and to a lesser extent the femoral tracts are now marked by the dark papillae beneath the skin. The ventral tracts are visible, but are less conspicuous because of the absence of dark color in the follicles. At this stage the wing is beginning to appear roughened, although no quills have actually broken the skin, and not only the remiges but some of their coverts can be distinguished.

Nestlings of 4 days normally have the wings almost wholly dark above and serrate along the posterior margins, because of the quills about to break through from beneath. All of the tracts on the dorsal surface are more pronounced, the cervical spinal tract having become broad and prominent, and the occipital region noticeably darker. Usually no quills have yet broken through the skin.

Young 5 days old have begun to look predominantly dark dorsally. Papillae are visible in all of the tracts, and a few quills may have erupted. First to appear are the primaries, which in advanced individuals may be about 1 millimeter long; the secondaries are close behind them in development.

Average nestlings 6 days of age have quills of the remiges protruding 2 or 3 millimeters; those of some of the coverts are about half as long. The quill tips of the rectrices are generally just appearing, and many of the quills have already erupted in the body tracts, both dorsally and ventrally. But the head and many other portions of the body still appear bare.

From about the 7th to the 10th days the nestlings become predominantly quill covered, as observed in the nest, although the tips of the feathers breaking from their sheaths are increasingly prominent as the quills themselves elongate. The quills of the capital tract may not be fully erupted until about the 8th day. Ventrally, plumage of the cervical, sternal, axillar, and anterior abdominal regions develops rapidly; but that of the interramal and submalar regions, along with the smaller feathers of the caudal tract (upper and lower coverts and anal circlet) is retarded. Most nestlings have reached 8 days of age before the quills in the latter regions are prominently exposed. The crural tract is also slow in development. By the 9th or 10th day, however, virtually all of the quills have made their appearance, and those of the flight feathers are very long and conspicuous. From approximately the 7-day stage on, some of the quills can be found breaking away at the tips so as to expose the feathers themselves. This seems to occur first on the flanks, along the lower edge of the femoral tracts, then in the broader portions of the ventral tracts, then in some of the secondary wing coverts, in the humeral tracts, and in the dorsal region. At about 8 or 9 days, on the average, the tips of the rectrices and remiges are freed from their sheaths for perhaps a millimeter. The unsheathing process in the other tracts follows much the same sequence as the original appearance of quills. Not until after 9 or 10 days are the feather tips of the capital tract, the interramal and submalar regions, and the tail coverts likely to show conspicuously. By this time the age of young is best determined by the measurements of feathers and of their unsheathed tips (see beyond).

From about the 11th through the 14th day, there is a steadily increasing smoothness dorsally, as the quills become more and more concealed beneath the feathers. By the end of this period, even the frontal region of the head normally appears smooth. The quills in the wings and tail may be only slightly visible when the birds are at rest. An area on the upper breast, however, and much of the lower belly are still bare.

In young of over 15 days, the body plumage appears completely developed, although the feathers are continuing to elongate and the sheaths to break away. Even after 20 days the tips of the folded wings fall short of the tail tip by several millimeters, and both the wings and the tail are considerably less than their adult length.

It is unfortunate that Dingle (1942: 429) has perpetuated the ill-founded statement of Dickey that Rough-wing young "within one week . . . assume somewhat the aspect and plumage of the adults"; and that he goes on to describe young "at the time of leaving the nest" as "similar to their parents in size, feathering, and length of wing and tail." Dingle quotes Skutch as having described 13-day-old nestlings as "well-feathered," but still far from ready to leave the burrow. It is of interest to note that Maynard (1889-91) described and figured a Rough-wing nestling a few days old.

Postjuvenal molt. Very little is known about the Rough-wing's transition from juvenal to first winter plumage. The postjuvenal molt, like the subsequent annual molts, is known to be complete, and to take place "after the birds have migrated southward in September, or very likely while they move leisurely along in flocks" (Dwight, 1900: 230). This molt of course involves for the males (Dwight, *loc. cit.*) "acquiring the saw-toothed outer primary." Wayne (1910: 141) was mistaken in his notion that "young birds do not appear to moult the outer two primaries until they are more than a year old."

Two nestlings I raised in captivity in 1950 lived long enough to undergo part of their molt: and it seems that its order, at least, must have approximated that found in the natural state. By August 12 molt was in progress in both young, then about 56-57 days of age, and most evident on the underparts, where some entirely new feathers may still have been coming in on the belly and flanks. Each bird had at least one new under tail covert, and the younger had in addition the outermost greater wing covert in sheath on each side. By August 20 the molt of the primaries was under way, and proceeding normally from the innermost outward, the corresponding coverts being also shed successively. On this date the younger bird had primaries "1" and "2" fully replaced, "3" nearly full length, and "4" still in sheath, in both wings; most of the greater coverts were in quill, the outer one on each side new, and the inner one or two not yet shed. The longest tertials were coming in. Heavy molt was continuing in all of the ventral tract forward to the breast, and in the femoral tracts. A few new quills were visible on the forehead just behind the base of the bill, and heavy molt was going on in the spinal and humeral tracts.

By this time the older bird was in very poor health, and its molt already lagging. That of the younger, however, proceeded for a time in apparently normal fashion. When its new primaries "4" were nearly grown (August 26), most of the greater coverts were approaching full length, two or three outer middle coverts were coming in, and there were some new quills, toward the outside, among the lesser coverts. No secondaries had yet been lost. The central pair of new

rectrices were just appearing. Several of the upper tail coverts were in quill. There was scattered molt visible on the forehead and front of the crown, all along the back, and in the humeral tracts. Below, molt was continuing in all tracts, and extending almost to the throat. By the time new primary "5" was coming in on each side, the outer pair of secondaries were also appearing, the longest tertial was completely replaced, and the greater coverts were nearly all replaced. The center rectrices were not yet full length, but many new quills were visible in both the upper and under tail coverts. Scattered heavy molt extended over the entire upper parts, including the rump, neck, and sides of head. The molt of the ventral tract was reaching the lower part of the throat.

Finally, both captive birds were in such obviously poor condition that I ceased keeping notes. At that time (September 8), in the younger, rectrices of the second pair were appearing, and the upper tail coverts were mostly replaced. Nearly all of the greater wing coverts had completely developed. Molt on the head was extending backward and medially toward the center of the crown, and a few new quills had appeared in the auriculars; heavy molt continued along the back and on the back of the head. In the ventral tract, the molt had progressed to the central part of the throat. By October 12, when the latter of the two birds died, the replacement of its body plumage was nearly completed; but that of the remiges, and particularly of the rectrices, had never progressed much beyond the stage last described. Unfortunately, the outer primaries were never shed.

To my knowledge, the plumage of the first winter does not differ essentially from subsequent ones, except for the retention of a few pinkish juvenal feathers in the chin and throat. The primary serrations are present, although often comparatively weak. During the postjuvenal molt, the contrast between the pale cinnamon-tipped juvenal feathers and the much darker incoming ones, with their pale gray margins, is very striking.

I should emphasize that the feathers (of adults as well as young) are slightly darker brown when freshly molted than they appear in spring birds, and that there are delicate pale edgings, particularly on the wing coverts and tertials but to some extent on all the dorsal body plumage, which are largely lost after a few months' wear. Birds in the fresh, slightly veiled plumage have an altogether richer appearance than do breeding individuals; but such specimens are not seen alive in our latitudes, nor are they apparently very common in collections. Sharpe and Wyatt (1885-94: 636) were so impressed with the difference as to describe a "distinct winter plumage," which is shown in the figure (*op. cit.*: Pl. 125). Most recent authors have

disregarded the point. Griscom (1929: 68), however, calls attention to the importance of understanding seasonal changes in deciding taxonomic questions.

MEASUREMENTS

I recorded measurements (at regular or irregular intervals) of about 48 young of known age, representing 11 broods. "Wing-length" as I use it here is in very young nestlings the length of the fleshy portion of the hand (Baldwin, Oberholser, and Worley, 1931: 86); while with the increasing development of the primary remiges it becomes essentially the chord of the wing (*op. cit.*: 76). "Tail-length" might be better designated here as "length of longest rectrices" inasmuch as the measurement, especially on small young, was not taken in quite the standard way (*op. cit.*: 92, 99); but in flabby nestlings the two measurements were scarcely distinguishable. The length of tarsus and the width of gape were ascertained in the customary fashion (*op. cit.*: 107, 21). Additional data I took were on the length of longest primaries (*op. cit.*: 88), usually about the fourth or fifth (though this was not kept entirely consistent), and on the greatest length (approximately) of rectrices and of remiges broken out of the feather sheath.

Comparative growth in body and plumage. The six young in Nest 11 were measured almost daily during their nestling period. In Figure 9 are plotted the wing, tail, tarsus, and gape measurements for this normal brood. The daily recorded values for individuals are plotted against age (not against date). Because of the scattering of data by age differences, satisfactory curves for the brood average cannot be based upon means of the plotted points alone. I therefore connected the plots for each individual by straight lines, interpolated values at half-day intervals between, and included these when computing the averages. The resulting curves are relatively smooth, and truly representative of all members of the brood. For the gape and tarsus, on account of the small dimensions and relatively large observational errors, the average curves alone most clearly indicate the trends.

The width of gape and length of tarsus increased together, and reached a maximum by about the tenth day. (The gape is actually wider in 10-day young, by nearly a millimeter, than it is in those a few days older.) It thus appears that during the first 10 days or so of nestling life the growth of skeletal elements and of soft parts is virtually completed. Supplementary evidence is presented in Table 9, where I give additional measurements from a series of 14 preserved specimens: young ranging from newly hatched to 12 days, and a single adult female. The forearm and hand may continue to elongate

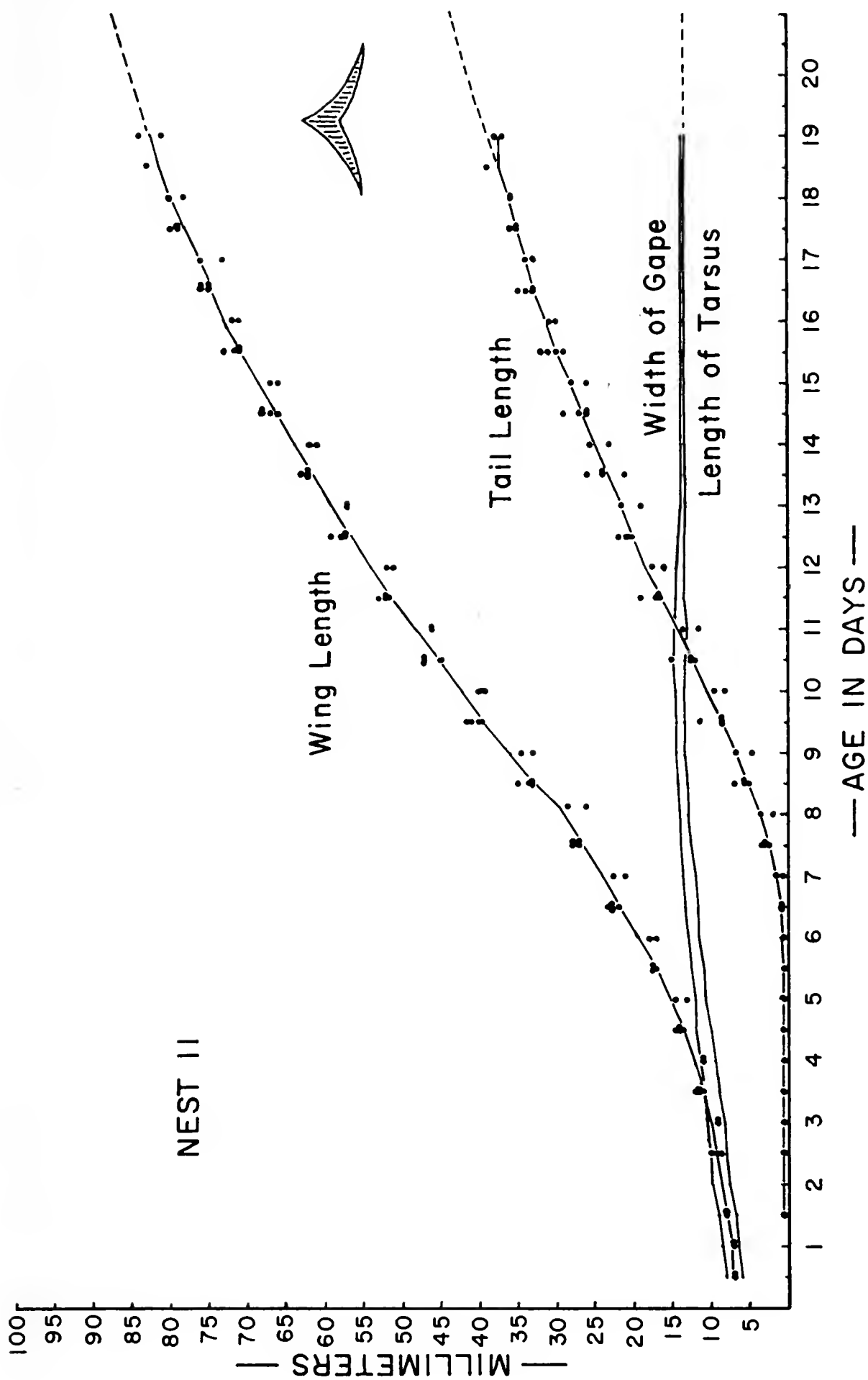


FIGURE 9. Linear measurements of six young in the brood of Nest 11 (1949) during their period of nestling growth. Points indicated are daily recorded measurements, plotted against individual age. Curves are based on calculations for each day and half-day, making use of interpolated values for individuals (see text). The shaded arrow indicates approximate ages of young at nest leaving.

TABLE 9
 REPRESENTATIVE MEASUREMENTS OF A SERIES OF PRESERVED SPECIMENS,
 OF KNOWN AGE AND FROM DIFFERENT NESTS

Age in Days		0	1	2	3	4	5	6	7	8	9	10	11	12	Adult Female
Nest Number		79	63	76	75	64	82	65	77	68	63	76	68	77	59 or 60
Linear Measurements (millimeters)	Tarsus	5	5.5	6	7.5	9	10	10.5	11.5	12	12	12	13	12	12.5
	Forearm	5.5	6.5	7.5	9	10.5	13	15	19	22	23	24	25	26.5	26.5
	Bill from Nostril	1.6	1.8	1.9	2.5	2.5	2.8	2.8	3	3.5	3.5	3.9	4	3.7	5.3
	Hand	5.5	7.5	8.5	10	12.5	14	17	20	22.5	23	24	25	25.5	24.5
	Tibiotarsus	7.5	9.5	10.5	12.5	16	17.5	19	20	22.5	22.5	22	23	22	23
	Skull Length (total)	12	14	14.5	16.5	18	18.5	19.5	21.5	23	23.5	24	24	25	27.5
	Body Length (approx.)	17	20	22	25.5	30	32	36.5	42	44	44	46	48	48	46.5
	Hind Claw	.8	1	1	1.4	1.6	2	2	2.5	2.8	3.2	3.2	3.5	3.5	4.5
Hind Toe with Claw		2.7	3.8	4.2	5.5	6	6.5	7.5	7.5	8.2	8	8	9	8.5	9.5

for as much as 12 days. The only body measurements distinctly less for the 12-day specimen than for the adult, however, are the total length of skull (from occiput to bill tip), length of bill from nostril (Baldwin, Oberholser, and Worley, 1931: 16), length of hind toe with claw (*op. cit.*: 111, 114), and length of hind claw (*loc. cit.*). These discrepancies are largely accounted for, since the rhamphotheca and claws, along with the feathers, are to continue development far beyond the age of 12 days. In young Barn Swallows, Stoner (1935: 407) found that bony growth was most rapid during the first 9 or 10 days, and (*op. cit.*: 403) complete by the 12th day. In Cliff Swallows (Stoner, 1945: 216) bony growth was nearly complete after 10 or 11 days, although (p. 211) a small amount was detectable thereafter.

The wing length (Figure 9) increases along a smooth curve, for by the time the hand has finished growing the rapid elongation of the primaries is in full swing. The tail-length curve does not begin to rise until about the 6th day, at the time of the eruption of the rectrices. Thereafter, it is similar to that of wing length, though the absolute rate of increase is less. By the time the young leave the nest, the growth of both wing and tail has slowed somewhat, and adult measurements cannot be reached for a considerable period. (Wing length averages approximately 110 mm. for adult male Rough-wings, and 103 mm. for adult females—see above; tail length averages about 50 mm. and about 47 mm. for males and females respectively—Ridgway, 1904: 59.)

Extent of variability. The variation within the single brood (shown in Figure 9) arose largely from differences established very early in development. The higher plots in this case apply to the younger members of the brood, and the two oldest (though actually a little larger on any given date) appear to lag when data are plotted for absolute ages.

The weights and measurements were always taken during the evening. All nestlings judged to have been hatched later than noon of the same day were considered for present purposes as newly hatched, all those hatched during that morning (roughly from midnight on) were grouped as one-half-day old, those hatched the previous afternoon (noon to midnight) were considered as one day old, and so on. Ages are thus indicated to the nearest half-day with a very small percentage of error.

I have less complete growth records on about 38 individuals of 9 1950 broods; and in Figure 10 certain data for these are plotted collectively with those for Nest 11. The extremes of observed variation are shown (vertical lines), and average curves drawn. Here I felt that for some individuals there were too few plots to warrant interpolation of intermediate values, and calculated all means from

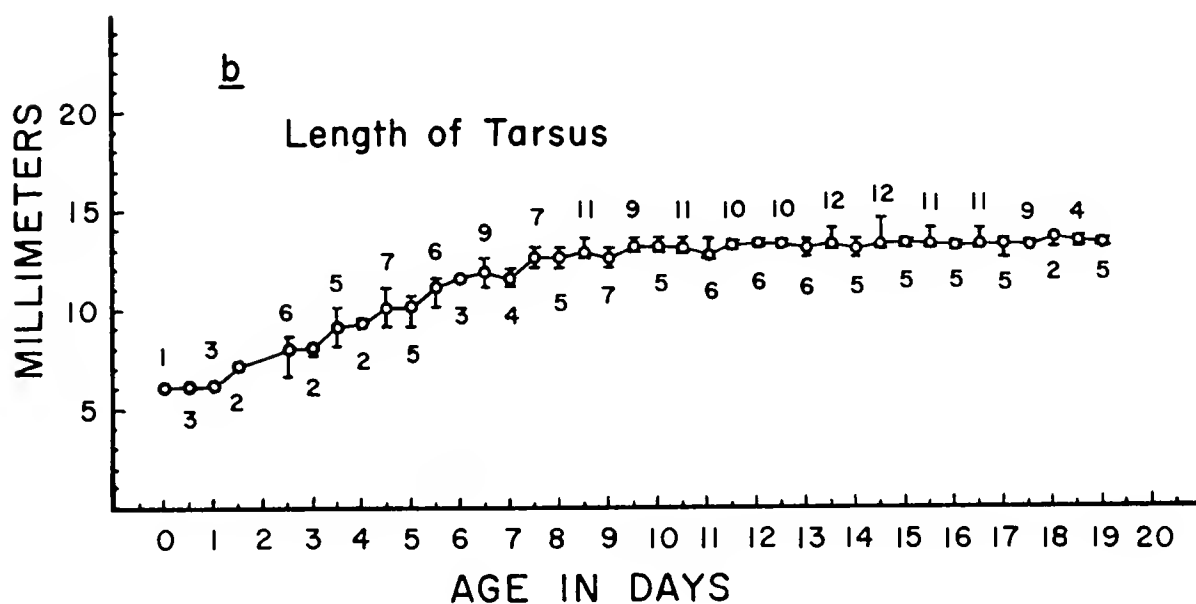
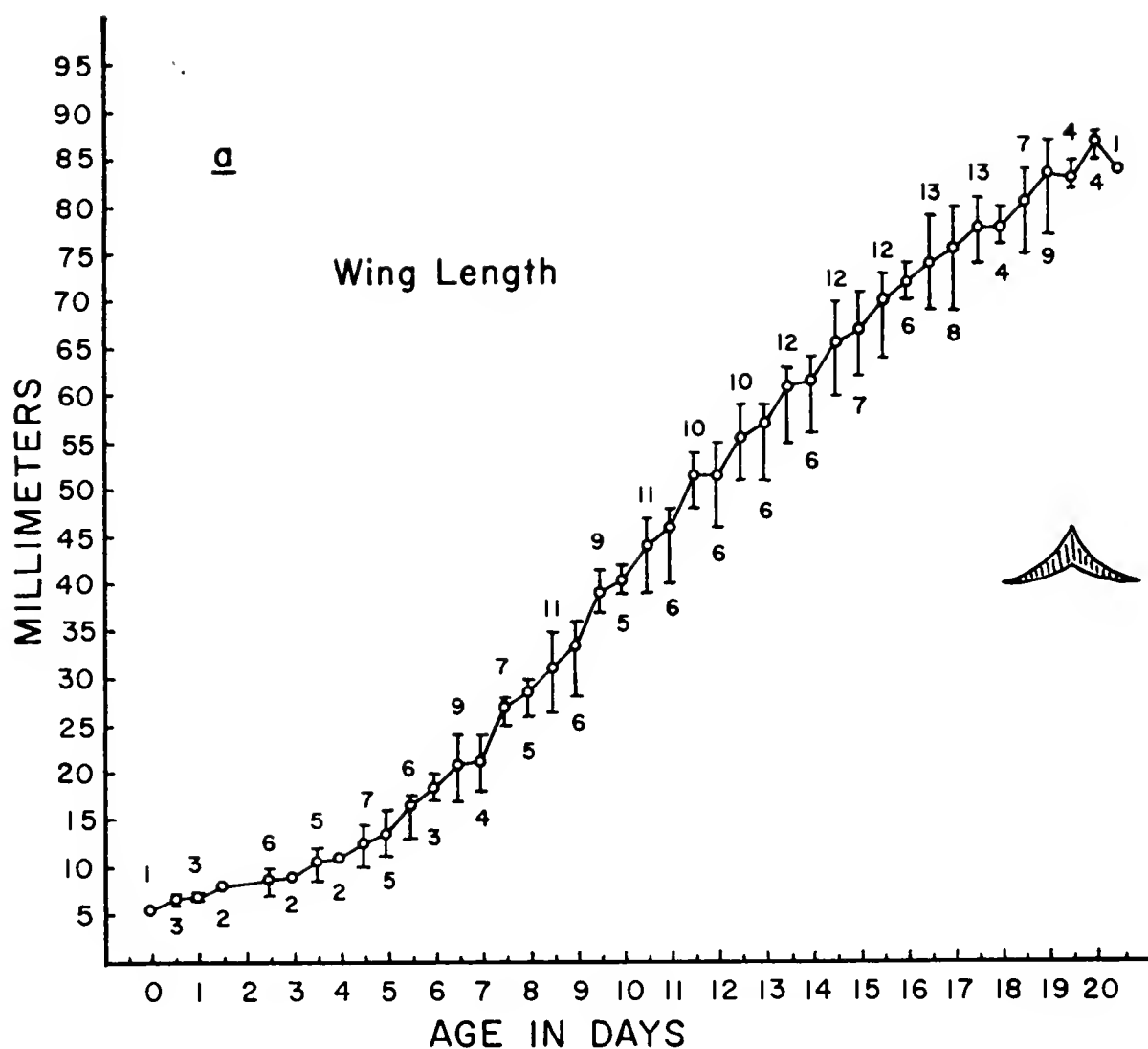


FIGURE 10. Curves showing increase of average wing length and tarsal length during nestling development, based on all appropriate measurements of the young studied. Circles represent means of recorded data for the various age groups, these being connected by solid lines. Vertical lines show observed ranges of variation; small figures indicate the size of samples used. Shaded arrow indicates approximate average ages of young at nest leaving.

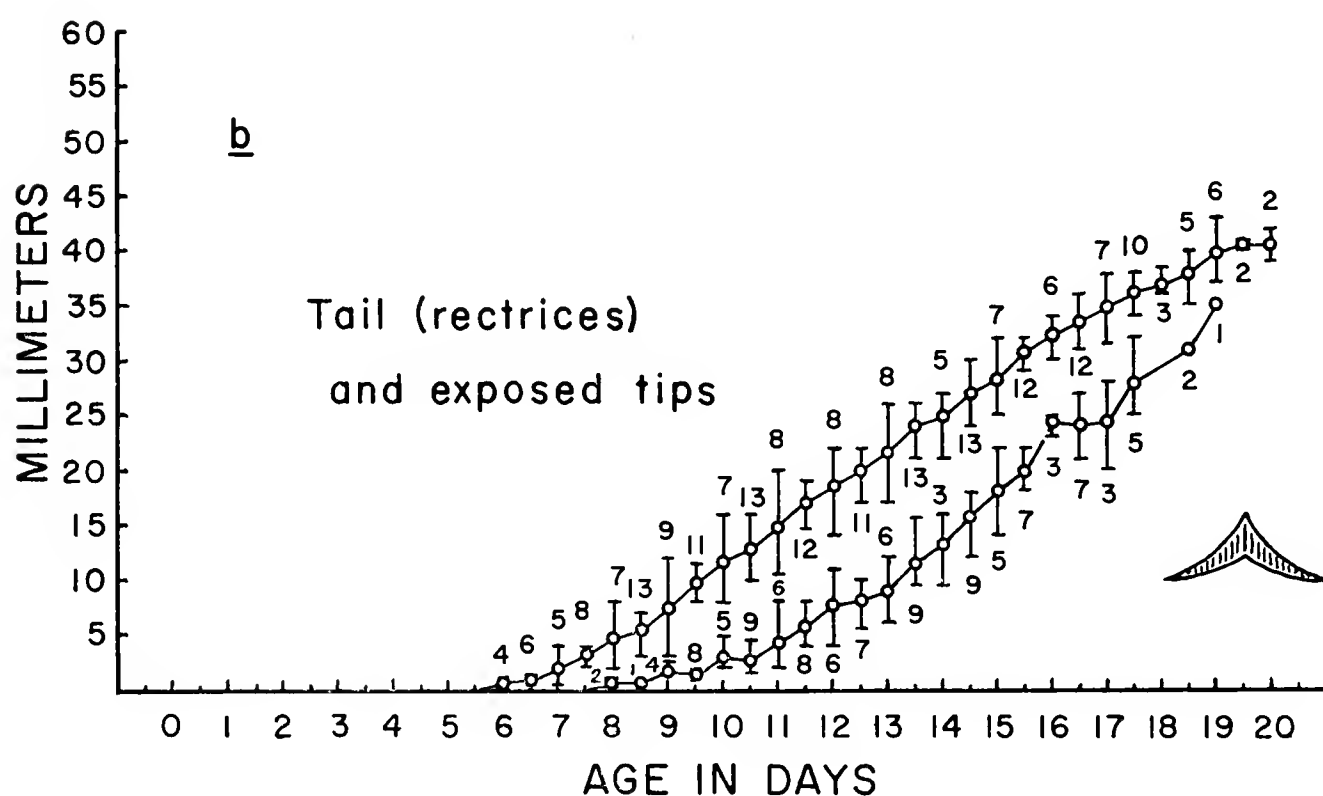
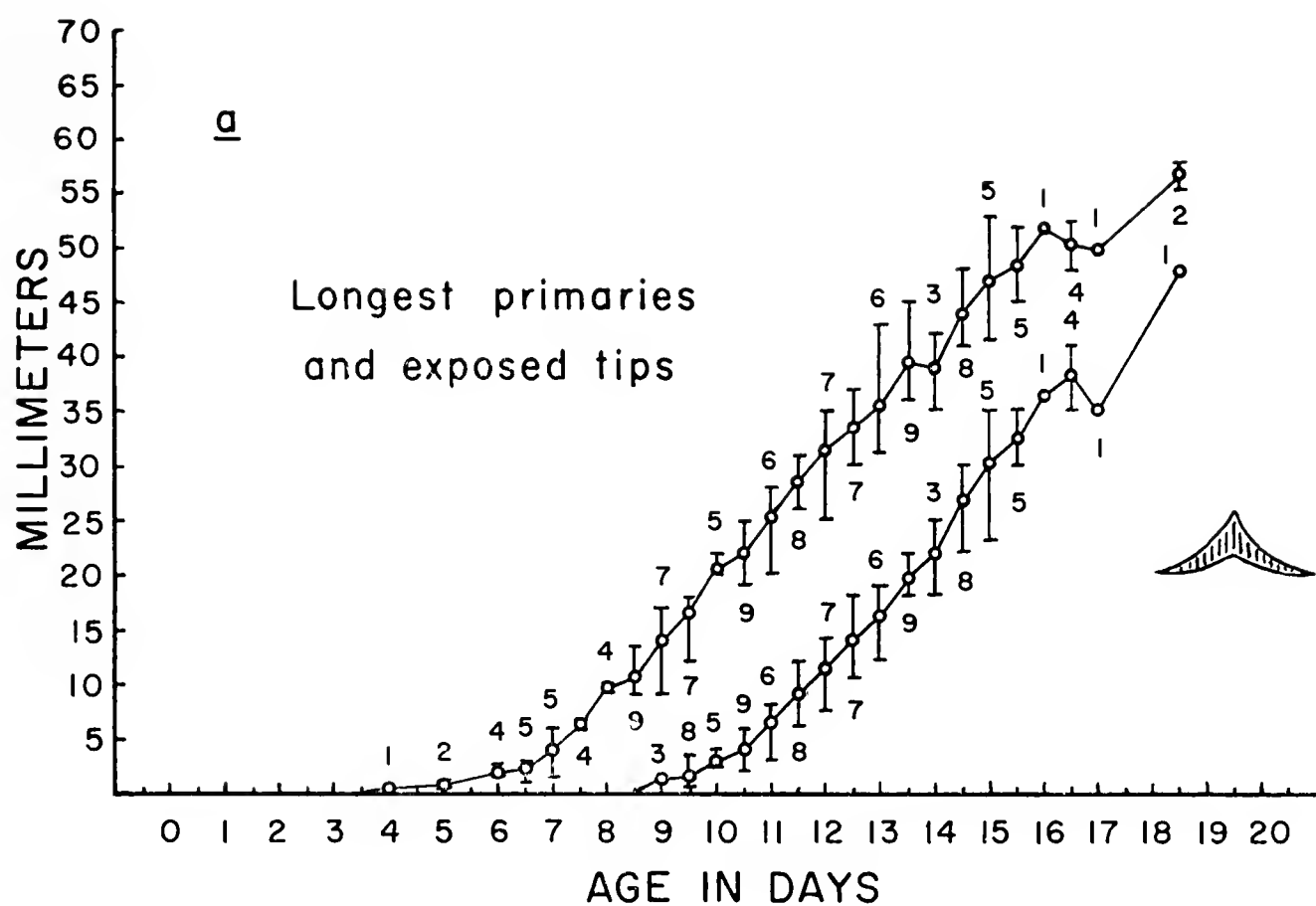


FIGURE 11. Curves showing (a) increase of average length of longest primaries and their webs freed from the quill, and (b) average length of rectrices and their exposed webs, during nestling development. Circles represent means of appropriate data, for all young studied; these are connected by solid lines. Each vertical line shows the observed range of variation within a group; small figures indicate sizes of samples. Shaded arrows indicate approximate average ages of young at nest leaving.

recorded measurements only; the size of the sample falling in each age group is indicated. Figure 10*a* shows the variation in wing length at any given age to be seldom over 10 millimeters, even for the older nestlings. Figure 10*b* suggests the very small range of variation in tarsal length.

The data in Figure 11, presented in the same way as those in Figure 10, are based upon measurements of about 39 representatives of the same 10 broods. The upper curves in *a* and *b* show the simple elongation of the flight feathers, in wings and in tail respectively, continuing at nearly constant rates from a day or two after the eruption of the quills to approximately the 16-day stage, with a gradual slackening of growth thereafter. The primaries grew at an average maximum rate of a little over 5 millimeters a day, the rectrices at an average maximum of about 4 millimeters a day. The lower curves show the rate at which the tips of the webs broke out of their sheaths. The tips of the primaries usually became exposed when the quills were some 12 to 15 millimeters long. The unsheathed tips of the rectrices were usually visible when the latter reached somewhat more than 5 millimeters. In a given individual, the webs of rectrices tended to appear a little before those of primaries. Once begun, the unsheathing process roughly kept pace with the elongation of the quills.

I plotted separately the wing-length data for members of large and of small broods, and for the older versus the younger members of broods, and was unable to show any differences in the characteristics of the average curves. It appears that, so long as the food supply and general nest conditions continue approximately normal, dimensional growth proceeds at a fairly uniform rate. It is affected by a moderate degree of individual variation, of which the causes are not determined; but not to any demonstrable extent by minor differences in external factors, such as ordinary competition from nest mates.

WEIGHT CHANGES

General patterns of gain and loss. Lack and Lack (1951: 537-539) have considered the developmental requirements of the Common Swift in comparison with those of other birds; they state that the nestling differs from "a small passerine bird of comparable size" in having "a peak nestling weight well above, instead of similar to, that of the adult." This distinction needs to be qualified where nestling swallows are concerned. Even though less extreme in swallows than in swifts, a parallel specialization in the two aerial groups is noticeable. Edson (1930) treated briefly the subject of regular weight loss by nestlings, using broods of House Wrens and of Violet-green

Swallows for his comparisons. Earlier, Stoner (1928b: 312-313) had noted a decrease in the weights of young Bank Swallows, after a peak was reached, and considered it "due primarily to a resorption of fat." In a subsequent paper he called attention (1936: 158) to "the more cancellated condition of the bones and the shrinking of the oral and other membranes," and to changes in size and capacity of the stomach. Reduced water content in body and plumage must also be a factor. Similar findings are reported by authors for all species of swallows studied. Growth curves for the young always show a rise to a peak weight above that of the adult, followed by an irregular downward trend for the rest of the nestling period.

In 1949 I recorded daily weights of 2 broods of Rough-wing nestlings during most of their growth period. In 1950 I weighed the young of 9 nests throughout the nestling period, but at somewhat longer and less regular intervals. Lack and Lack (1951: 520) have given reasons, which apply equally well in the present case, for the selection of late evening as a regular weighing time. Most of my weighing was done during the period from 5:30 to 7:30 p.m. Lack and Lack (*op. cit.*: 520-521; 531-534) have treated the nightly weight loss of nestling swifts, and the small daily fluctuations in the weight curves. I have not seen detailed graphs drawn for any swallow species. We may assume that substantial loss of weight takes place each night, and that during the period of rapid growth the previous level is reached and passed early the following day (Edson, 1939: 13, and 1943: 402; Braey, 1946: 189-190). The analyses to follow do not take such minor fluctuations into account.

In Figure 12 are shown the growth curves for the brood of Nest 20 (1950), with individual weights plotted by date as recorded, and connected by straight lines. The older nestlings tend to be heavier on any given date; and curves continue approximately parallel until their peaks are approached. During about the latter third of the nestling period there is a general but very irregular loss of weight, and curves of individuals tend to become indistinguishable on the basis of relative age.

For making comparisons, it is much more useful to plot the data against the actual ages of the respective young. The curves drawn in this way for Nest 20 are shown in Figure 13. Making adjustments for age differences complicates the problem of constructing a smooth curve of *average* weight for any given group, unless intermediate weights of individuals are interpolated before computing a mean for each point. The assumption that changes between weighings took place along a straight line is of course not entirely valid, but it is the only one possible under the circumstances.

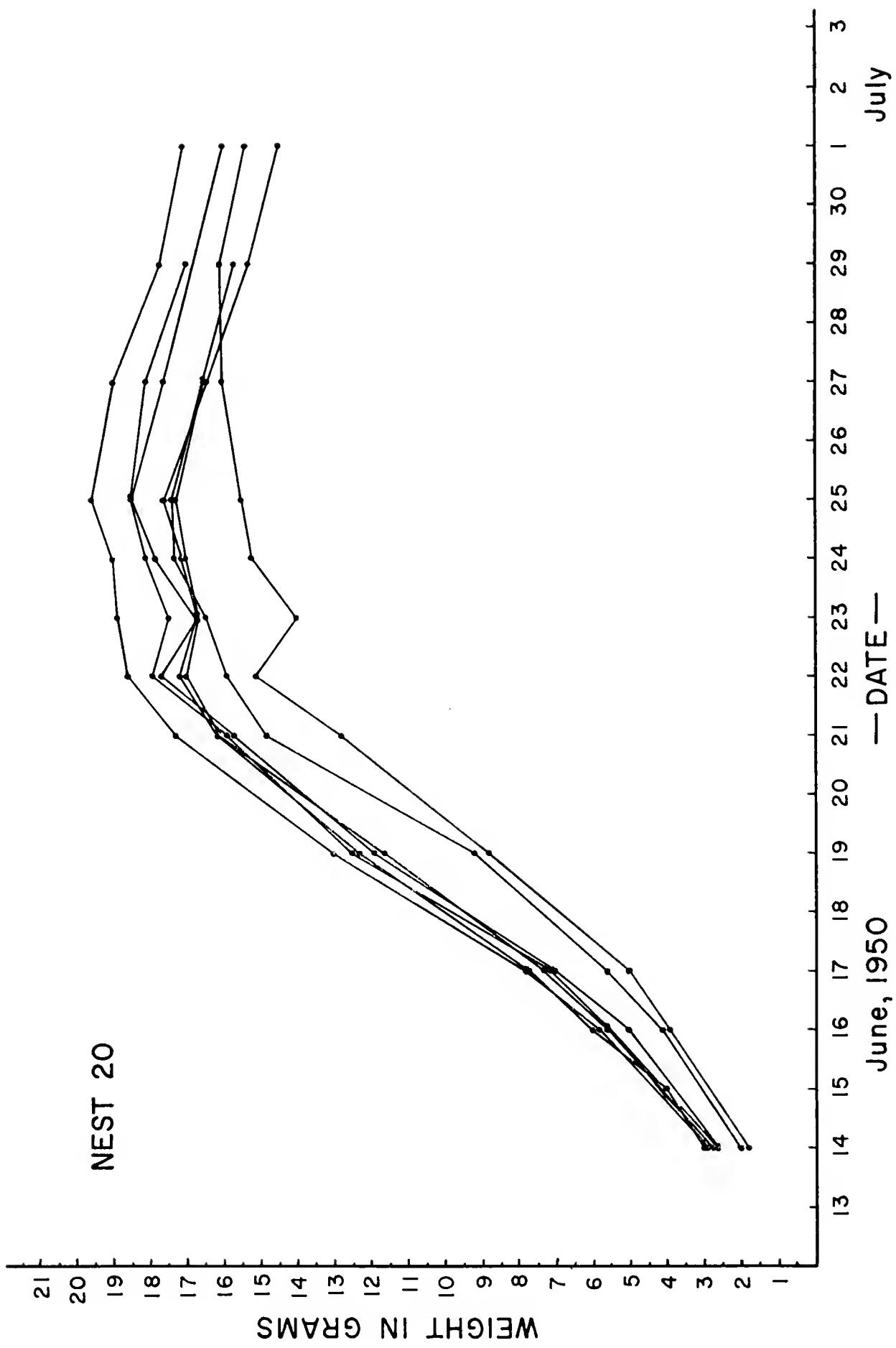


FIGURE 12. Curves of weight change for the 7 members of the brood of Nest 20, plotted against actual dates. The points show weights recorded on the days indicated; adjacent points for each individual are connected by straight lines.

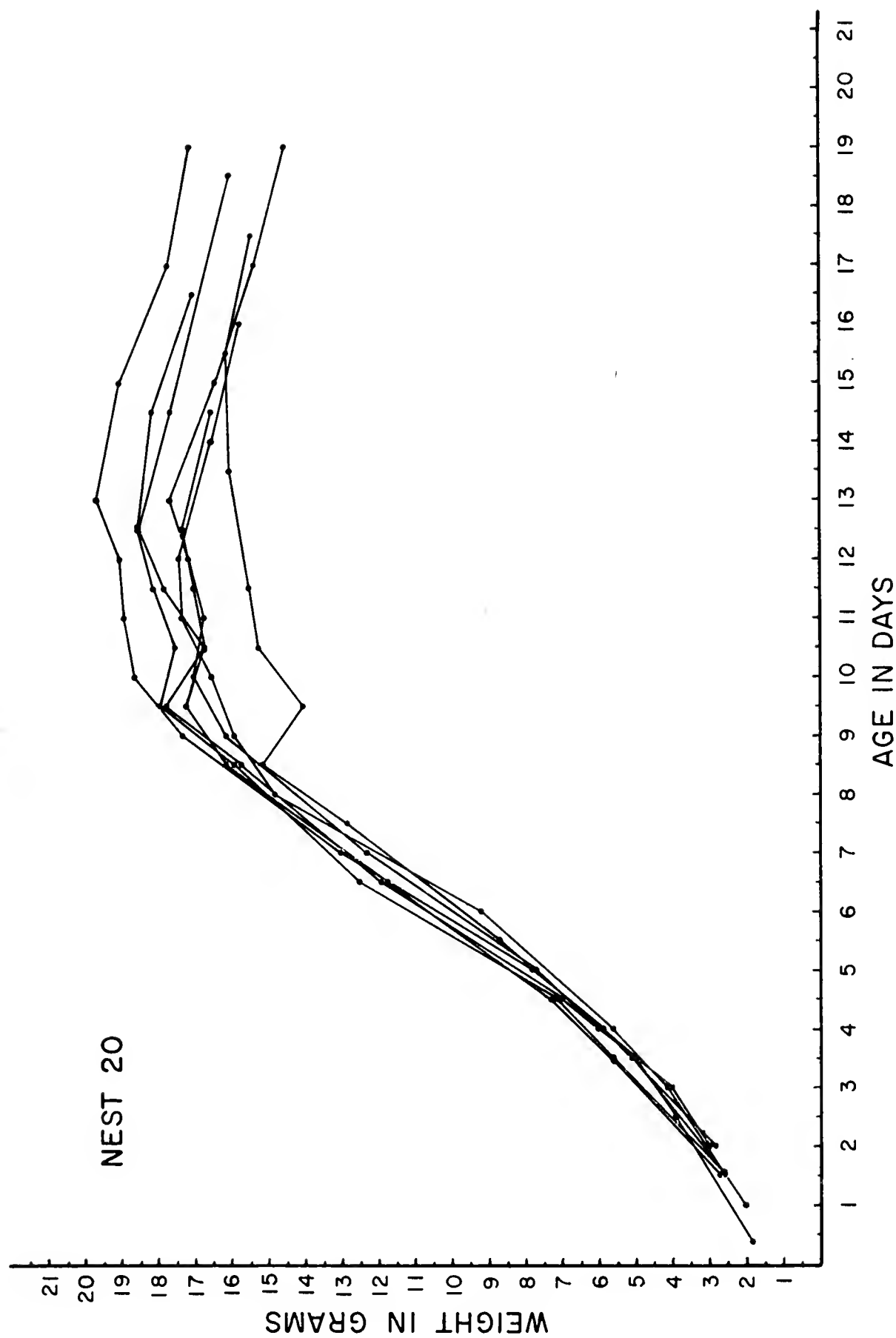


FIGURE 13. Curves of weight change for the 7 nestlings of Nest 20, plotted against individual age. The points show weights recorded, their relative positions (cf. Figure 12) depending upon age differences at the time of weighing; adjacent points for each individual are connected by straight lines.

Figure 14 represents a composite curve for all the nestlings studied. It is based on weights of 61 young weighed periodically in the field, and of 17 additional young collected. The vertical lines indicate the observed range for each age group. The circled plots in the figure represent means of the recorded weights only. The number above each point gives the size of the sample. The curve is based also on the very large number of additional values interpolated. The horizontal dotted line represents the mean adult weight, which is reached between the 9th and 10th days, and passed again on about the 16th, according to the average curve. Inconsistencies toward the right-hand end of the curve are due to an increasing scarcity of data as the young approached the time of nest leaving.

Factors causing variation. Two factors which seemed likely to account for part of the observed deviation from the means were brood size and relative age of the individual in the brood. To test the effect of the former, I drew the pair of curves in Figure 15, where data for the 6 broods of 4 and of 5 young, including 28 individuals, and for the 5 broods of 6 and of 7, with 33 individual young are plotted separately. The plots are means based on recorded weights only; the curves were smoothed by interpolation of additional figures. Members of the smaller broods grew faster (averaging some 10 per cent heavier during the whole period of weight gain), attained maximum weight about a day earlier (average peak on 12th instead of on 13th day), and reached a peak weight averaging over 0.5 gm. higher, than did members of large broods. It appears that the smaller broods also lost weight a little earlier and more rapidly. In his study of nestling Tree Swallows, Paynter (1954: 108-110) obtained strikingly similar results.

Curves representing growth of the older and of the younger individuals in the various broods show only very minor differences. Forty nestlings, including all those hatched within one day of the oldest member of the brood, were arbitrarily separated as "older." The remaining 21 "younger" nestlings, from the 11 broods, all had hatched a day or more after the oldest. The two curves in Figure 16a for these two groups nearly or quite coincide at many points. Birds of the "younger" group, however, appear to have started growth a little more promptly, and to have tapered off less abruptly than their older siblings, so as to reach approximately the same maximum a day earlier (average on 12th instead of on 13th day). They then began to lose weight considerably more rapidly. In 7 nests, only one or two of the brood hatched as a first half-day group; in 4 nests, the last young hatched 2 days or more after the oldest. Data pertaining to these two groups, of 12 and 4 individuals respectively, are used in Figure 16b. The samples were very small; but it appears that the trends just

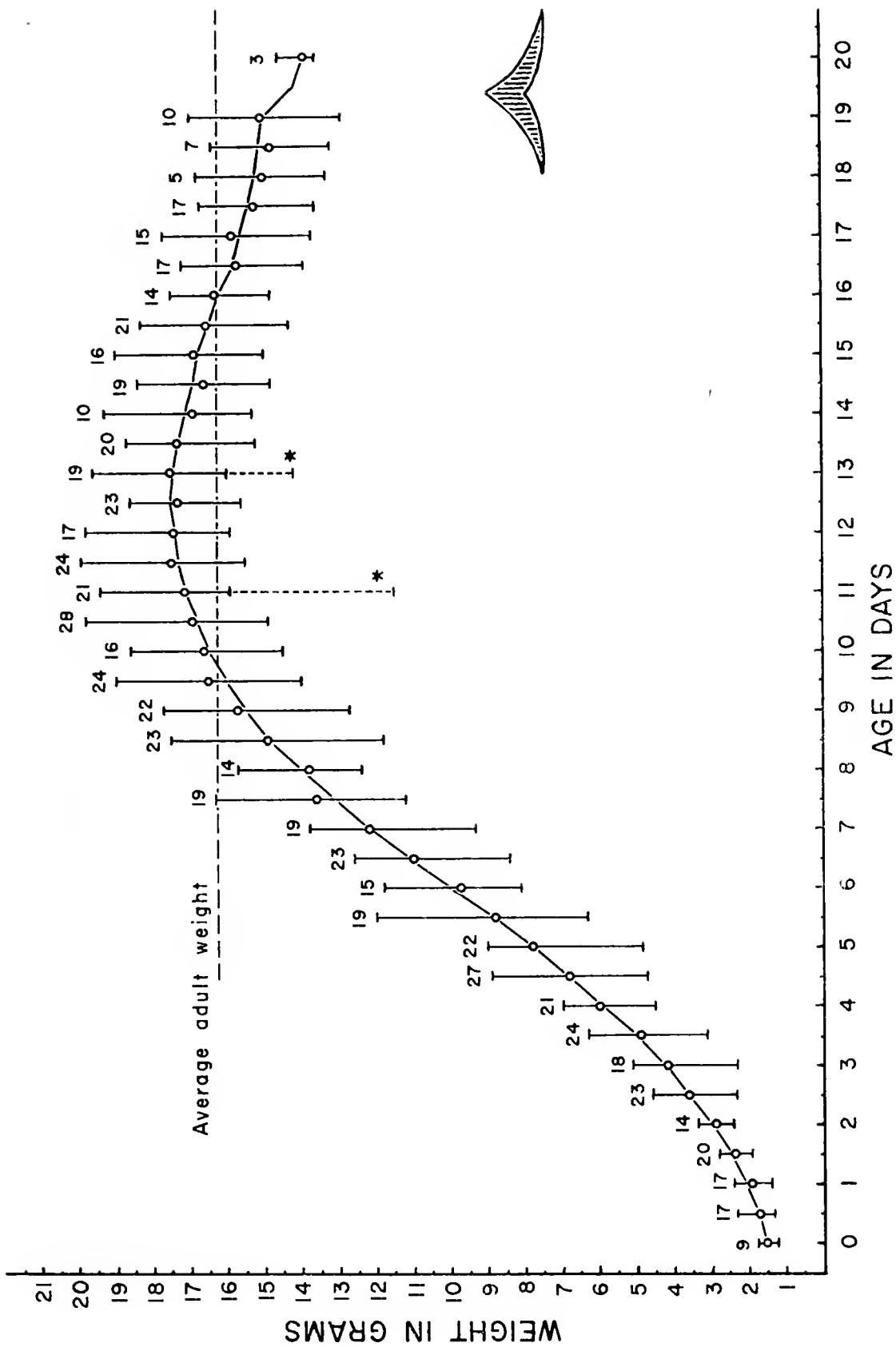


FIGURE 14. Average weight changes of nestling Rough-wings studied. Incorporated are 712 recorded weights taken from a total of 78 individuals representing 20 broods. Circles represent mean values, based on all weights recorded for respective age groups; vertical lines show observed ranges; figures indicate the size of samples. The curve is based on averages of recorded weights, plus those interpolated from individual curves of 61 nestlings (see text). (Plots indicated by asterisks and dotted lines represent weights of the same individual (in Nest 27), which was decidedly subnormal and appeared temporarily sick.) Shaded arrow indicates approximate average ages of young at nest leaving.

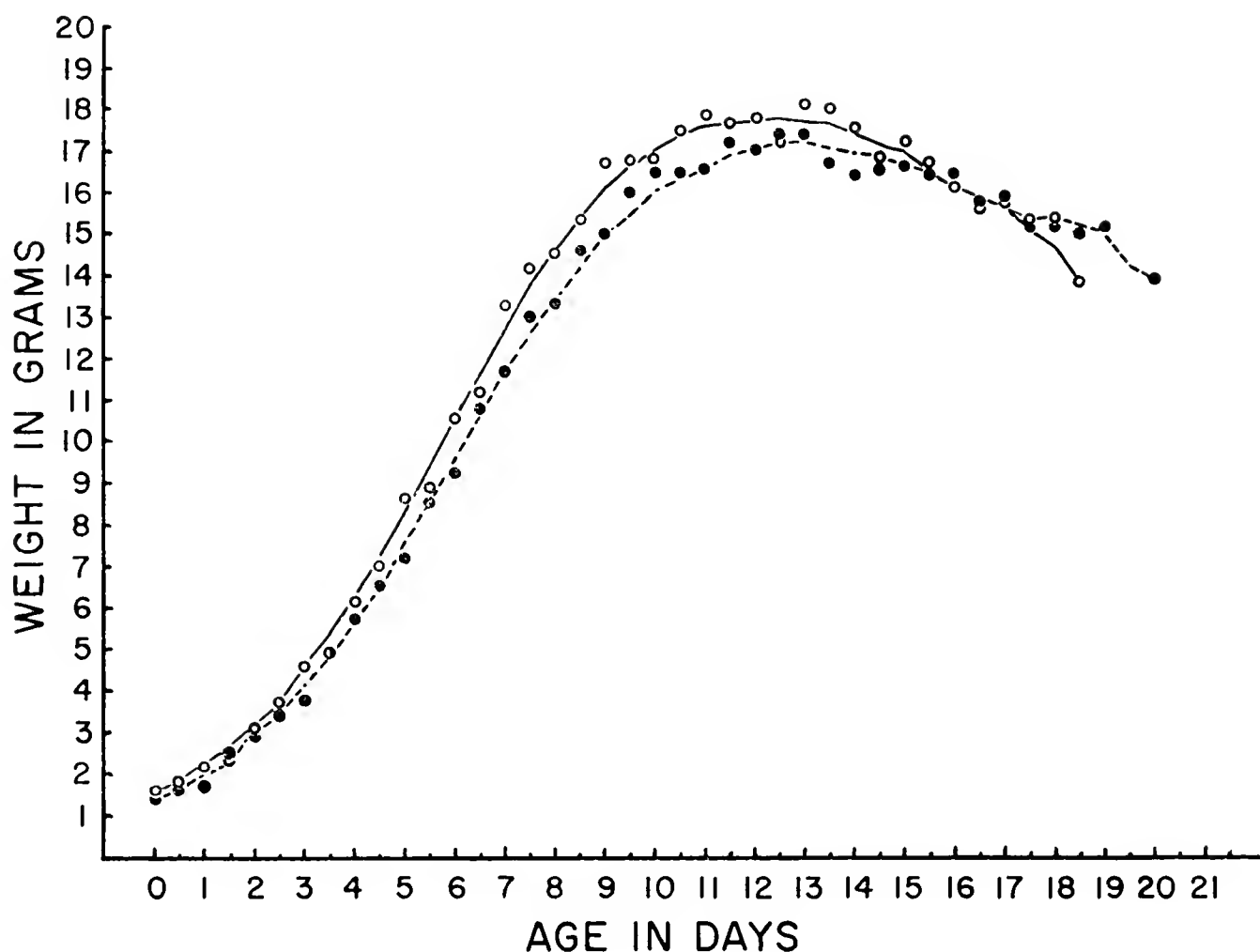


FIGURE 15. Comparison of average weight curves for nestlings in smaller and in larger broods. For 28 young in 6 broods of 4-5, mean recorded weights are indicated by open circles, and an average curve (using interpolated weights as well — see text) by a solid line. For 33 young in 5 broods of 6-7, mean recorded weights are shown by solid dots, and the average curve by a broken line.

described are accentuated. The youngest individuals, after a prompt start, grew a little more slowly at first, but reached a peak $11\frac{1}{2}$ days earlier (at $11\frac{1}{2}$ instead of 13 days of age, on the average) than the oldest. They then lost weight more rapidly.

Differing degrees of competition from nest mates thus probably affected certain characteristics of the weight curves, and account for part of the observed variation.

Individual weights. Curves based on mean weights tend to obscure certain features of the individual curves, and a few supplementary comments may be useful.

Weights of 9 young considered as newly hatched range from 1.2 to 1.7 grams, with a mean of 1.48 grams. Initial weight appears to be a function, in turn, of egg size. Conspicuously small young hatched from the first and third eggs laid in Nest 22, both of which had been previously noted as small. In Nest 29, the first egg was strikingly large, and the nestling weighed 2.0 grams when barely one-half day old, this being the second highest recorded for that age.

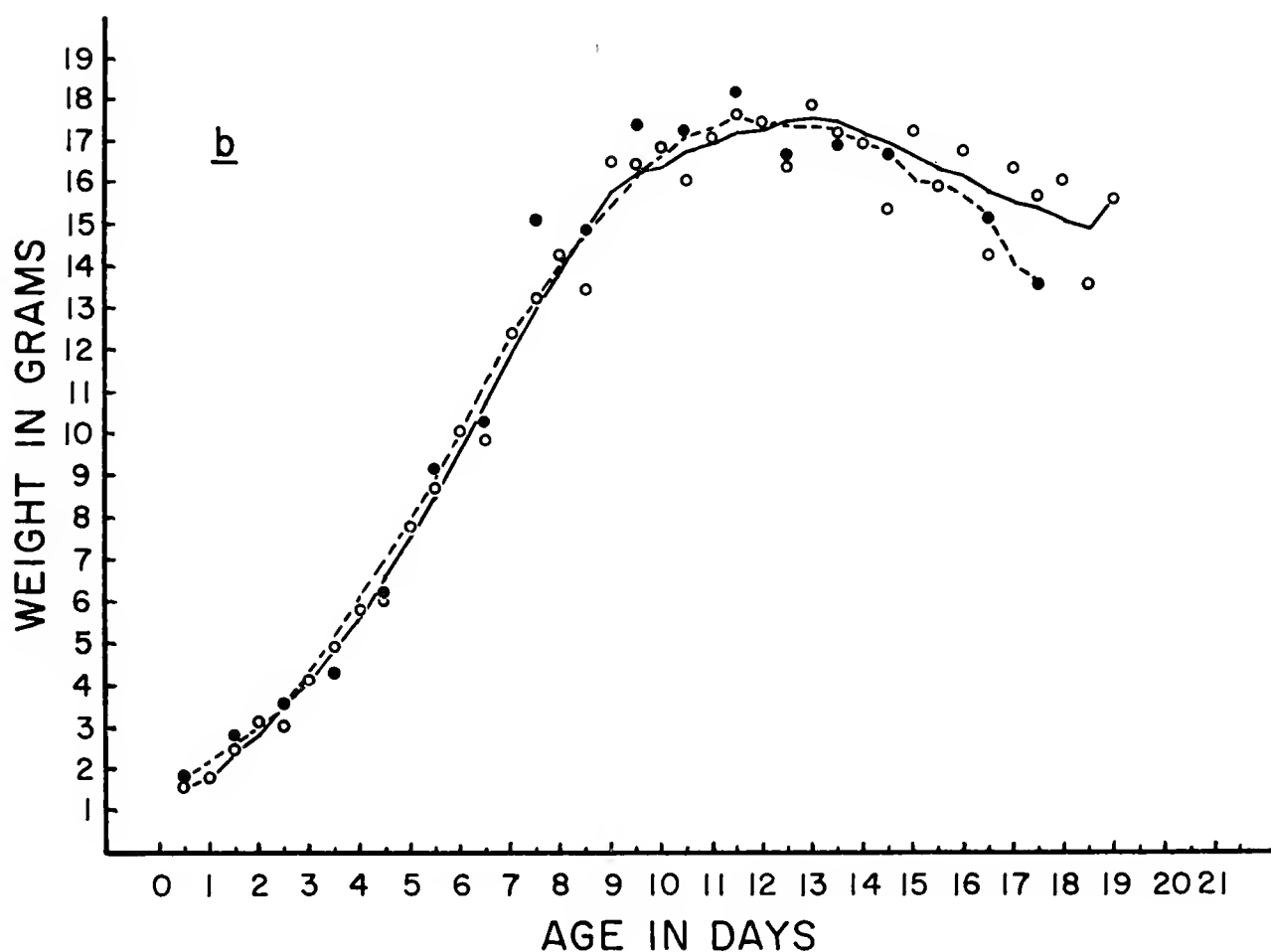
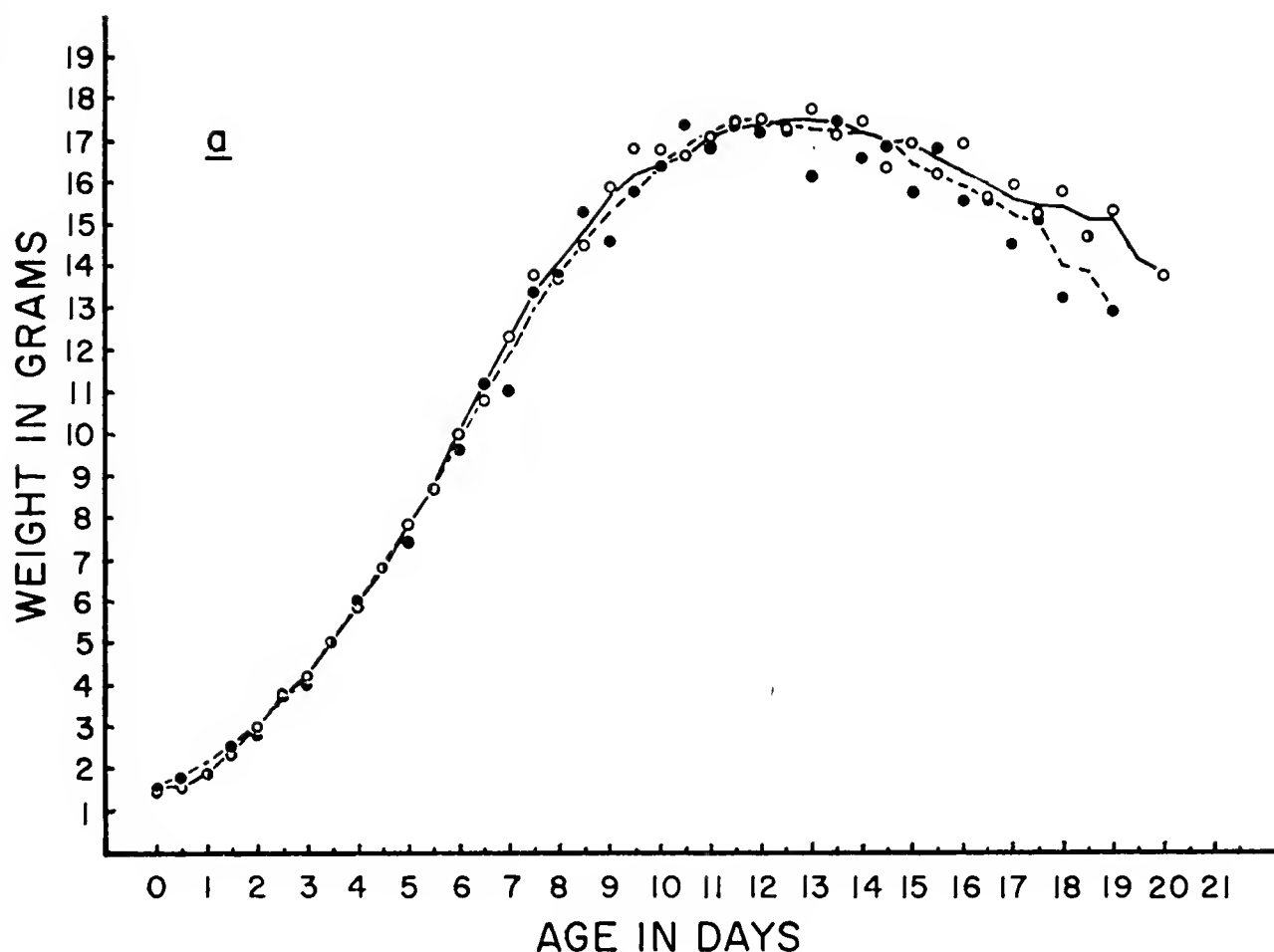


FIGURE 16. Comparisons of average weight curves for older and younger members of the same broods. In *a* are treated the 40 oldest members, and the 21 youngest, of 11 broods (for basis of division, see text). In *b* are treated only 12 individuals (in 7 broods) which hatched distinctly ahead of nest mates, and 4 individuals (in 4 broods) which were distinctly behind siblings in hatching (see text). In each case, open circles and solid line represent mean weights and curve (by interpolating individual weights—see text) for the older members; solid black dots and broken line refer to the younger members.

In some instances relative weight at hatching is indicative of the relative weight maintained throughout the nestling period: the highest half-day weight recorded and the highest observed maximum were both for the same individual. In other cases, early trends do not seem to be maintained: in Nest 29, the large hatchling just mentioned was not recorded at as high a peak as the other three in the brood.

Some individuals begin immediately after hatching to gain weight rather rapidly. Others have continued for a day or two with very little change, presumably not having received much food. In some broods the youngest birds have shown this slowness in starting, possibly as the result of direct competition. In at least as many cases, however, older individuals, perhaps not receiving a full quota of food until others have also hatched, have been so retarded. During the most rapid growth, a rather uniform gain of about 2.0 grams per day is to be expected. The largest gains recorded, all 3.1 grams in a day's time, were for the second youngest in Nest 11 (from $6\frac{1}{2}$ to $7\frac{1}{2}$ days), the youngest in Nest 12 ($5\frac{1}{2}$ to $6\frac{1}{2}$ days), and the oldest in Nest 25 ($5\frac{1}{2}$ to $6\frac{1}{2}$ days).

At an age of about 8 to 10 days most individual curves show a sharp break (almost completely masked in curves based on mean values). The rapid growth appears to be suddenly arrested, and in many cases there is a distinct *drop* in weight, before the increase is resumed at a slower rate. This does not appear to have been noted in growth studies of other swallows (cf. Petersen, 1955: 264; Paynter, 1954: 106). Where the break is ill defined, or absent, the peak weight is attained at a somewhat earlier age. This is most common among members of smaller broods, and especially noticeable with some of the youngest individuals in broods.

While it is improbable that I recorded the actual peak weight for all individuals, Table 10 shows some simple data on recorded maxima, broken down with respect to brood size and relative age in brood. These figures corroborate findings outlined above. There is a slight difference between the early and late members of broods, and greater differences between broods of 4-5 and of 6-7. Members of the smaller broods reach a higher peak, and reach it earlier. The last young to hatch, even in large broods, suffer only a temporary handicap, if any. They reach almost the same maximum weight as their older nest mates, and tend to do so at a slightly earlier age (though this is not uniformly the case).

After reaching its maximum weight, every individual studied lost weight during the remainder of its period in the nest. As a rough check on fledgling weights, I arbitrarily used all last-recorded individual weights (a total of 38) which were taken at an age of 17 days or more. A few of the young were weighed as late as 19 days, and

TABLE 10

DATA ON MAXIMUM RECORDED WEIGHTS REACHED BY NESTLINGS

Group	Highest Recorded Weight, Grams			Age of Maximum Weight, Days		
	Total Range	Mean Weight	Size of Samples	Total Range	Mean Age	Size of Samples ¹
All Young	15.6 - 19.9	17.76	61	9 - 17	12.4	68
Broods of 4-5	15.6 - 19.9	18.05	28	9 - 14	11.8	30
Broods of 6-7	15.8 - 19.6	17.51	33	10 1/2 - 17	12.9	38
Older ²	15.6 - 19.6	17.79	40	9 - 17	12.5	47
Younger ²	15.9 - 19.9	17.69	21	10 1/2 - 15 1/2	12.2	21

¹ Where the same maximum was recorded more than one day, ages for all were included.

² For explanation of division, see text.

three at 20 days. The mean value of these "final" weights is 15.0 grams, at an *average* age of 18.1 days. Among the young in the sample, 32 (84 per cent) had lost at least 10 per cent of their maximum recorded weight when last weighed, 19 (50 per cent) had lost at least 15 per cent, and 5 (13 per cent) had lost 20 per cent or more. The smallest loss was 4.3 per cent, and the greatest was 23.1 per cent, both by birds last weighed at 17½ days.

Based upon the adult mean, about 16.26 gm., the nestlings appear to reach an average weight about 9.2 per cent above the adult average, and then to drop to about 7.7 per cent below it, before leaving the nest. I have no information on the trends after departure from the nest.

Significance of the findings. Lack and Lack (1951) have regarded the very high peak weights attained by nestling swifts, and the extreme variability of the peak and of the time required to reach it, as a sort of buffer against failures of food supply during the long nestling period. My studies provide no clearcut evidence as to whether such a mechanism is effective to some extent among swallows. Differences in weather conditions and in food supply during the period of growth were presumably at a minimum among these broods, most of which were developing at about the same time, and all the broods mentioned could be regarded as showing about "normal" development.

It should be pointed out, however, that the time required for a nestling to complete the major part of its body growth (approximately 12 days) is about the average period for reaching maximum

weight. Thereafter the growth of dermal structures continues unabated while the weight undergoes more or less extreme fluctuation and reduction. It appears significant that I have found the weights more variable and more obviously affected by minor environmental influences than the linear measurements. Judging by the relative flexibility I have demonstrated in the weight curves, even at early ages, it seems probable that considerable irregularity in feeding would result merely in modified fat deposition or absorption, and have no appreciable effect on the growth of body and plumage elements. Certain individuals that I observed to undergo unusual weight fluctuations were otherwise developing normally for their age. Only under extremely adverse conditions were all the growth processes retarded, and then death finally resulted.

PHYSICAL AND BEHAVIORISTIC DEVELOPMENT

Many changes in growing nestlings are intimately associated with the general body growth. I have made no detailed study of the developing psychological reactions, yet certain prominent behavior traits, appearing at various ages, could not be overlooked in the routine handling of the young.

Changes in bill, feet, and soft parts. In newly hatched nestlings the bill and feet are entirely flesh-colored. After a day or two a darkish tip appears on the bill. Within 5 or 6 days the entire medial portion appears bluish- or purplish-brown, still with a dark tip, and blending into the cream-colored, fleshy margins of the gape. By the time young leave the nest, their developing rhamphothecae are largely fuscous, as in the adult. The mouth lining is always yellow, appearing to be brighter in small young than in older nestlings and adults. The egg tooth is prominent at the time of hatching, and my series of preserved specimens indicates that it persists in part until the time of nest leaving. It is discernible as a minute prominence just behind the tip of the tomium, even in specimens as old as 19 days. (Clark, 1961, makes no reference to the egg tooth in Hirundinidae.) As the scales of the podothecae, distinguishable at hatching, grow and develop, the toes are first to darken, turning purplish at about 4 days. The tarsi remain largely pinkish until about the 7th day; as their growth is completed they become increasingly brown and, along with the toes, finally fuscous. The soles of the feet remain somewhat paler.

The eyes are first opened at about 5 days. The change, however, is gradual: at first mere slits are visible, and these only occasionally, so that the eyes must be scarcely functional. After perhaps 7 or 8 days, the young can truly hold their eyes open for a period; but it is several days longer before they are open continuously, and the blue

haziness of the eyeball gives way to a more alert expression. The iris then has become dark brown.

Posture and activity. For the first few hours after hatching, the normal position of young is doubled forward, with the head resting close to the breast. As soon as they emerge from the shell, however, they are able to raise the head momentarily to beg. Their attitude remains largely sprawling for 9 or 10 days. As they gradually gain the use of their legs (from 5 or 6 days on), they first progress merely by pushing themselves forward, in a prone position, toward any convenient sheltering object.

When only a week old, nestlings can crouch for a time with the head erect. After about 10 days, they are able to sit fairly erect, with feet under them and heads up, and to progress with a shuffling walk. When released at the entrance of a burrow, they promptly scuttle back into the nest. Not until they are nearly two weeks old can they perch with any degree of assurance on an object of small diameter, and until nest leaving they are most at home on a flat surface. Begging movements are apparently confined to the head and mouth for about two weeks. Only at about 15 days did captive young begin to quiver their wings in begging for food. The means by which nestlings in a cramped burrow get exercise sufficient to strengthen their wings for flight remains something of a mystery. Not until they reached an age of over 20 days were our captive birds observed to exercise their wings deliberately, although the wing fluttering that accompanied their begging had become increasingly vigorous.

Response to disturbance and handling. For about the first 5 days, the young Rough-wings were always found lying motionless and silent in the nest during my regular inspections. When handled, they made little or no effort to resist. At the next stage, while young were from about 5 to 8 days of age, they normally called loudly, and begged, as I approached the hole and examined the contents of the nest. This behavior stopped abruptly; by the time they reached 8 or 9 days, nestlings would utter only a few notes as I approached, and then crouch down quietly but alertly. After 10 or 12 days, they characteristically pushed as far back against the end of the nest chamber as possible (cf. Skutch, 1960: 270). At ages beyond about 15 days, nestlings showed increasing signs of nervousness when handled. On a few occasions, they exhibited what appeared to be a reaction of extreme fright, becoming almost paralyzed, with head drawn in, wings folded close and held forward, and toes clenched. Several seconds were required for the birds to regain their equilibrium after release, and to move back into the nest. Toward the last, the behavior of broods disturbed in the nest changed once more.

Instead of crowding back into the burrow, some or all of the individuals might attempt to fly out. The actions of the young, therefore, often give a rough indication of their age.

Call notes of nestlings. Very small young utter only a single high, thin peep. I have heard this from individuals begging for food only a few minutes after hatching. The characteristic food call of older nestlings, probably from about 5 or 6 days on, is a much louder, harsher, and frequently repeated note. This is dry and rasping, not unlike the corresponding notes of young Bank Swallows, an insistent “*cha-cha-cha*.” Blake (1947: 293) has compared the call of young Rough-wings, half grown or older, to “the very faintest hiss of escaping steam.” Broods nearly ready to fly can be heard calling loudly when fed; and the sound, to my ear, is not fundamentally different from that made by much younger nestlings. Individual young, however, from about 11 or 12 days of age on, commonly give voice to a single very short cry, apparently an alarm note, which has a quality strongly suggestive of the adult call: softer, more rolling, and more nasal than the food call of smaller young. On a very few occasions I heard an additional call, a sudden, sharp “*churk*,” expressing extreme alarm or perhaps pain, as when an individual was actually grasped to be taken from the nest, or accidentally hurt by the claws of a struggling nest mate. Skutch (1960: 270) states that a nestling past 13 days of age sometimes “opened its bill widely and hissed” as he inspected the burrow (in Guatemala?).

Feeding and drinking reactions, and general behavior. The two nestlings raised by hand afforded interesting sidelights on behavior. Their begging and manner of accepting food did not differ materially from that of other passerine nestlings we had raised. Their pecking instincts, as expected, were extremely weak and slow to develop — picking up food from the floor of a cage never did seem a natural movement. Their drinking behavior was especially interesting. When first confronted with a pan of water, or a shiny surface resembling water (at about 21 and 23 days of age), both birds stood back at a distance of several inches, awkwardly extended the neck with mouth open, bent forward, and several times shuffled a few steps ahead. They attempted to take water into the widely opened mouth by merely dipping the lower mandible. Finally getting a drop or so, they would then raise the head and go through exaggerated swallowing movements. After a time they learned to drink with less difficulty; but the whole procedure was obviously unnatural, and not the instinctive action it is for the average passerine fledgling. Similar difficulties were encountered when the two attempted to bathe in a dish. (Adult swallows, of course, both drink and bathe while in flight.) From a relatively early age, the young swallows were able to cling tenaciously

to steep surfaces, wherever they could get a foothold, and to climb actively, using the feet, wings, and even neck and bill to assist them, until they reached the highest point attainable.

DEPARTURE FROM NEST

NESTLING PERIOD

In view of possible ambiguity in referring to a *fledging period*, I prefer to use the term *nestling period* to indicate the time between the hatching of an individual and its departure from the nest. Should the strict definition of the former term be applied here (cf. Skutch, 1945: 11-12), it would be all but meaningless: young swallows are always capable of at least a limited flight for many days before they normally leave the nest. Furthermore, the frequent use of the word *fledge* to denote the act of leaving the nest — a usage which, even if acceptable, seems to me unfortunate — has introduced the danger of further confusion of terms.

It is difficult, without prolonged observations at individual nests, to determine accurately the nestling period of such a species as the Rough-wing. Unless the young are seen actually departing, it is necessary to examine each nest at intervals to determine their presence or absence, and this in itself is very likely to affect the times of leaving. In addition, the relatively great disparity that often exists in both the hatching times and the times of departure, among the several members of a brood, makes difficult the establishment of satisfactory standards. Since, in my study, a large proportion of the nestlings were marked, and of rather precisely known age, I have attempted to treat the information on an individual basis, rather than on a brood basis. Skutch, in considering such problems, has suggested obtaining at least satisfactory average figures, and ordinarily correct ones, by assuming (1945: 13) that "when nestlings do not all depart on the same day . . . they quit the nest in the order of their age." It has seemed reasonable to adopt a similar principle in the present analysis, in instances where it was applicable and necessary.

Age of leaving. The material in Figure 17 is based on records for 98 selected individuals, fledged in 20 nests, in 1949, 1950, and 1951. The horizontal lines represent roughly the ages at which certain young were known to leave the nest. Nest numbers are indicated, along with the total number actually fledged in each brood. Vertical dotted lines show the minimum possible spread observed among the members of single broods. The latitude of observational error (length of horizontal bars) is relatively great, being in each case the sum of latitudes for hatching and for nest leaving. Most of the estimates used, however, are correct to within one day or less and none involve

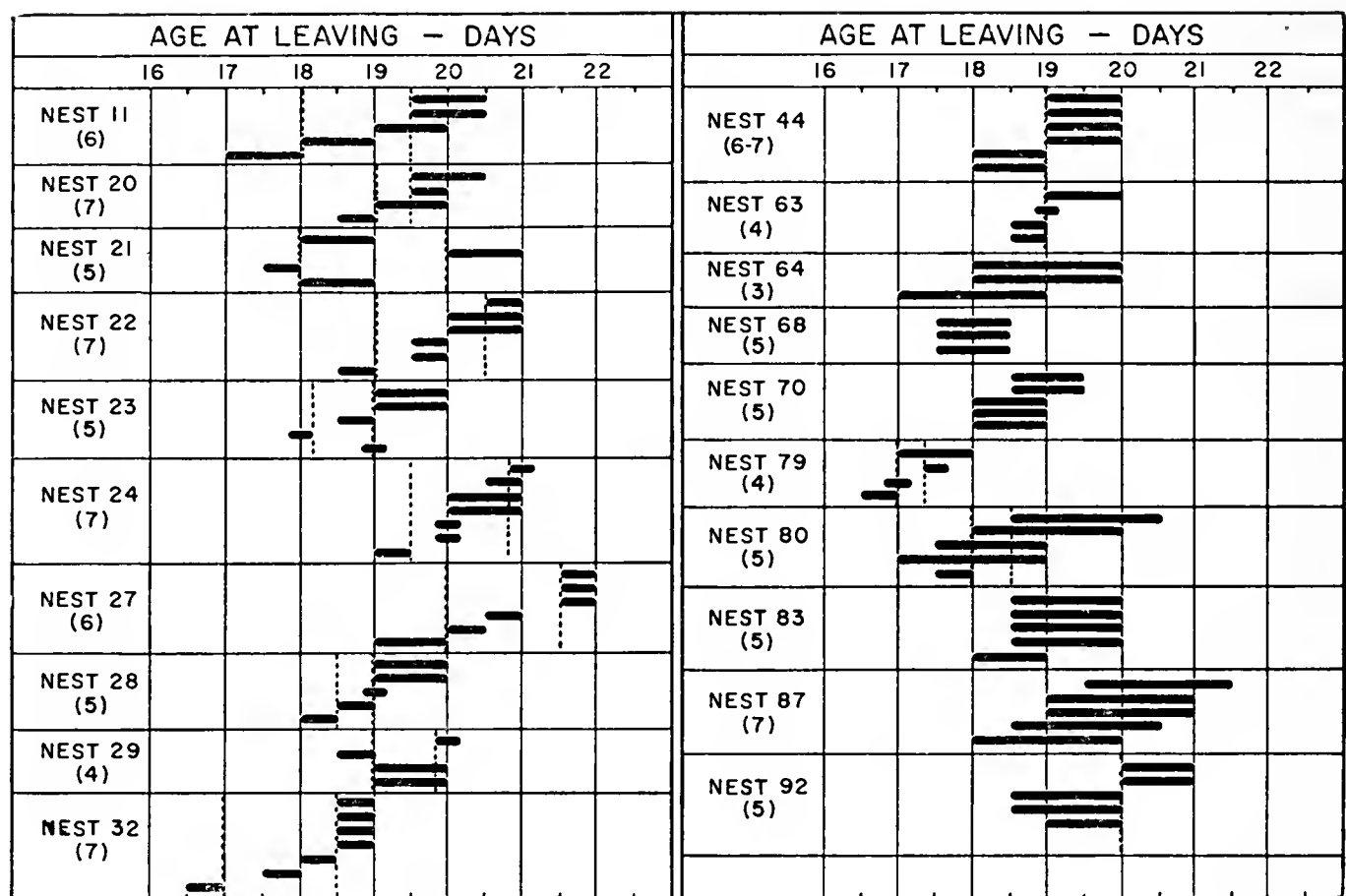


FIGURE 17. Approximate ages of 98 selected young, from 20 broods, at time of departure from nest. The length of each black bar indicates the margin of observational error (based on accuracy of knowledge both of hatching and of departure of the individual). Vertical dotted lines indicate minimum spreads demonstrated within each brood. Figures in parentheses give total size of the broods concerned.

ranges of possible error totaling more than two days. Approximate data obtained from numerous other individuals and nests have been useful for corroboration.

Most individuals left the nest at ages of between 18 and 21 days. Though a true average cannot be calculated, the mean nestling period for these young must have been between 19 and 19½ days. Dickey's reference (Dingle, 1942: 429) to young "ready to leave the nest, at the lapse of 12 days" must be the result of a serious misconception. The minimum age at which normal departure is proved to have taken place during my study is about 17 days. The maximum age at which any young are clearly demonstrated to have left is about 21½ days. I have no evidence that nestlings can have left (without disturbance) at ages of less than about 16½ days, or that any can have stayed beyond about 22 days. I have not considered cases in which my disturbance obviously had a direct effect; and I do not think it has greatly altered results. There is no evidence that the broods I was regularly studying showed any reduction of nestling period, as compared to others that I observed only casually.

The nestling period seems to be relatively short as compared to those of other swallows. Allen and Nice (1952: 630) have tabulated "length of fledging" figures for fourteen species of swallows, as reported in the literature. The period given for *S. r. fulvipennis* (quoted from Skutch, 1945: 21) is somewhat longer than mine for *S. r. serripennis*, 20-21 days; but this is based, I believe, on 4 members of only 1 brood (cf. Skutch, 1960: 271), and may or may not reflect an actual subspecific difference. If we accept a figure between 19 and 20 days as being typical for the Rough-wing in Michigan, there are only two species (both tropical) for which are listed nestling periods as low. That of the African Rough-wing *Psolidoprocne holomelaena massaica* is given as 25-27 days, almost a week longer. Among North American swallows, only the Bank and Tree Swallows seem to have comparable averages. Although the period of the latter appears (Allen and Nice, *loc. cit.*) to be far more variable, a subsequent study by Paynter (1954: 53 ff.) indicates a range and average closely approximating mine for the Rough-wing.

Just what elements determine the time of departure, I am not able to say. It is not possible to limit the nestling period in terms of either weight or linear measurements. I have frequently seen young Rough-wings, still several days from their expected time of nest leaving, prove themselves capable of more or less sustained flight. The indication on Figures 9, 10, 11, and 14, however, of approximate ages at which young leave the nest allows for an estimation of general relationships.

Spans of time and age. The younger members of broods (Figure 17, lower bars for each nest) tended to leave at an earlier age than the older members. If the young were nearly of the same age they tended to leave at least during the same day. If there was a wider discrepancy in ages, the course of events seemed to vary more from nest to nest. Sometimes the older members of the brood remained in the nest until the younger reached a normal age for leaving. Again, the younger might leave somewhat prematurely, along with the older. In still other cases, the departure of the various young was spread over as much as two days, usually taking place roughly in order of age. Thus the span of ages at nest leaving, within a given brood, may vary from no more than a few hours to at least two days. Since members of large broods are most likely to differ in age, they would be expected to show the more extreme irregularities in nestling periods. However, Figure 17 shows little correlation between brood size and absolute length of nestling period (cf. Paynter, *op. cit.*: 54-57).

In two instances, where the age range of young was wide, I found nestlings leaving and later returning to the nest. In Nest 21, one individual (omitted from Figure 17) was out at least two, and

probably three, separate times, beginning 4 days before the brood left for good; and two others returned at least once, up to 2 days after their first departure. Only part of this irregularity was due to my disturbance. On two successive evenings, young flew from Nest 22 after I had inspected it, and at least one of these later returned, before the brood finally left. The youngest member of the brood of Nest 20, although not abnormally young to be out, was found, the next evening after it had flown, in with the younger brood of adjacent Nest 27. My general findings, however, support those of Blake (1953: 107), who, with reference to the Rough-wing in Massachusetts, states: "What observations I have been able to make indicate that the fledglings do not return to the burrow after they have once flown from it."

NEST LEAVING

Behavior. Only on a few occasions have I been able to watch any young make their first flight under reasonably normal circumstances. The exact role of the parents in speeding the departure of the nestlings is not clear. The reduction in the rate of feeding (already described) may well play a part. I have seen nothing I would construe as active urging by either parent, except that there were periodic visits to the nest, with brief circling and calling close to the entrance, on the occasions when I knew that young were ready to leave (cf. Petersen, 1955: 259-260).

Although the young are surprisingly strong on the wing by the time they are ready to leave, their flight usually appears somewhat labored and aimless. It is likely to carry them directly away from the nest for as much as a hundred yards or so, at which point they come down, or perhaps are forced down, to alight clumsily on some tree or bush or on the ground. Some individuals, however, appear better coördinated, and at once circle about, much as do the adults. The presence of a number of adults is a characteristic accompaniment of nest leaving, which I have noted on a number of occasions. It appears that adult Rough-wings may assemble from some distance, so that far more are commonly in evidence, circling and calling, than are normally to be found in the immediate area. As a young bird leaves the nest, they crowd and pursue it, as if to urge it away and then down to some convenient perch to rest. This behavior has received comment by Skutch (1960: 271), who considers it of survival value to the young.

Most of my inspections were made in the evening or in the late afternoon; and by that time, in a great many cases, the young had entirely disappeared from the vicinity. This was to be expected if, as Skutch has found (1945: 10), "nestlings as a rule leave the nest

during the early hours of the morning, seldom in the afternoon, unless frightened by the observer." Such is not uniformly the case, however, for the departure of at least some undisturbed young I have observed took place in the afternoon.

Dates. We may refer to Figure 18 (below) for approximate dates by which young are normally out of the nest in the Ann Arbor area. Generally speaking, the majority have left the nest at the end of June and during the first two weeks of July, with the peak expected about the first of July. Extreme dates I recorded were June 21 (1952) and July 28 (1950). Only a few broods, presumably all the result of second nesting attempts, remained in the nest as late as the middle of July. Surprising, therefore, is the report by Hartley (O'Reilly *et al.*, 1954: 82) of a Rough-wing nest with three young on August 2, 1953, at Northville, Michigan.

YOUNG OUT OF THE NEST

In the great majority of cases, I found no trace of specific broods after their departure. I have seen many young birds still recognizable by their short wings and characteristic coloration flying and perching along with groups of adult Rough-wings. But in comparison to the numbers known to have been fledged they have been few indeed.

Parental feeding. I do not know for how long a period the young are dependent, or to what extent both parents may share in the final stages of caring for them. For a short time the members of a brood seem to stay together, usually accompanied by one or both parents, moving about freely over a wide area, but spending considerable periods perched in one or more groups on suitable fences, wires, or trees. When I have seen individuals fed, the young bird remained perched, begging with fluttering wings, while the parent either hovered beside it to feed, or also perched briefly. Grimes (1930: 5) described the feeding of a fledgling as observed by him in Florida, where both parents were present, and one was seen to feed the young bird, "alighting beside it to do so." Brewster (1907: 221-222) describes the feeding by the parents of young Rough-wings perched on a wire, in Massachusetts. His statement that they "must have been out of the nest for a week or more" is, however, open to doubt.

Roosting habits of fledglings. The few cases in which I observed young Rough-wings to return to the nest for a night or two must be regarded merely as irregularities. Nests I have inspected after all the young had left have always been empty. Once, at dusk, I flushed what appeared to be an entire brood (presumably those that had left that day from nearby Nest 24) from along a broken-down fence, closely sheltered by bushes and woods, where no doubt they were preparing to roost. There is no evidence that fledglings regularly return

to the nest once they have left it, except in those species that habitually roost in such situations (cf. Skutch, 1960: 285-286). Thus I have frequently seen young Bank Swallows re-entering their burrows. Young Purple Martins (Allen and Nice, 1952: 634), Barn Swallows (Owen, 1918: 227; Smith, 1937: 68), Cliff Swallows (Viotor and Viotor, 1912: 150), and House Martins (Lind, 1960: 106-107), for example, commonly return to the nest for resting or roosting after having flown; Violet-green Swallow young (Edson, 1943: 400) do so only occasionally.

POSTNESTING ACTIVITIES

Departure from nesting area. It has been found that as soon as young are on the wing the Rough-wings usually lose no time in quitting the area entirely. Although small groups linger for a few days in the general vicinity of the nesting territories, as appears from certain records I have of marked birds, there must be a general movement toward more favorable localities for feeding and for roosting, very likely in the vicinity of the larger lakes or rivers. There the Rough-wings perhaps join other swallows, and very shortly begin a gradual movement to the south. In Michigan as a whole, according to Wood (1951: 289), fall migration "apparently . . . takes place principally in July." I myself have no August record for the species.

My only distant banding return demonstrates the prompt departure and movement of one individual. It was banded (50-11439) as a nestling 17 days old, in Nest 27 on July 3, 1950; leaving the nest July 8, it was found August 13, 7 miles south of Dyersburg, Dyer County, northwestern Tennessee. I have been unable to obtain further information on the circumstances under which it was found. In the Fish and Wildlife Service files (A. J. Duvall, letter) is a similar record of a Rough-wing (43-38518) banded at Kitchener, Ontario, by Bergey, on June 24, 1945; it was killed on or before August 29 of the same year, at Bunkie, Louisiana.

Flocking. Except for the communal roosts already referred to, I have seen no evidence of what I would consider a flock of Rough-wings, though straggling groups of half a dozen to a dozen were commonly noted circling or perched. They seldom mingled with the large flocks of Bank Swallows that were so conspicuous about the gravel pits each July before their southward movement. Apparently it is mostly in small exclusive bands that the migratory flights are begun. Wood (1951: 289-290) quotes a number of observers in other parts of Michigan, who also have reported only small numbers, in no case more than "15 or 20" birds in a flock, during the autumn movements. However, Todd (1940: 369) cites a report of "a flock of two hundred" as far north as Presque Isle, Pennsylvania, on September 1.

Roberts (1932: 44) remarks that in Minnesota “in late August it mingles with the large Swallow aggregations and soon thereafter departs for its winter home in the Southland.” Skutch (1960: 271-274) describes at length the roosting of large flocks of Rough-winged Swallows, some of them possibly migrants from the North, in Costa Rican canefields in winter.

Part V

GENERAL ANALYSES

TIMING OF NESTING SEASON

The graphs provided herewith in Figure 18 have already been referred to as a means of placing some approximate time spans and peaks of activity in proper relationship. It remains to consider the year-to-year variation, and its correlation with weather conditions, during the period 1950 to 1952 at Ann Arbor.

In the figure, solid bars are used to indicate exactly determined dates, and open bars to indicate dates only approximately known, by inference from earlier or later observations. (Times estimated for nest leaving are likely to have the widest margins of error.) In 1952 I did not work regularly enough in the field to discover a few scattered nestings that may have taken place late in the season. My field work in 1949 was begun so late in the season that the data are of no value in the present connection.

Comparison of Figure 18 with the scattered nesting records given for Michigan by Wood (1951: 289), for Montana by Weydemeyer (1933), for Minnesota by Roberts (1932: 43-44), for Florida by Howell (1932: 331-332), for South Carolina by Sprunt and Chamberlain (1949: 364), and for several states by Dingle (1942: 433) has disclosed no notable inconsistencies. There is evidence of a limited latitudinal change, as would be expected, in the time of earliest laying. The discussion to follow concerns my own observations over a limited period, and is on a purely local basis.

EVENTS IN THE BREEDING CYCLE

Arrival. It would be interesting to know how much the actual time of the Rough-wings' arrival varies from year to year, and whether it could be correlated with, for example, mean temperatures, as Allen and Nice (1952: 608-612) have done for that of the Purple Martin at Ann Arbor and other points. The Martin arrives considerably earlier. Moreover, it is likely to be much more concentrated and more conspicuous on arrival. During my field studies, fluctuations in early activity around potential nest sites, from day to day and from year to year, were clearly correlated with general weather conditions. During persistent cold, rainy, snowy, or windy spells, the Rough-wings were little or not at all in evidence. But at

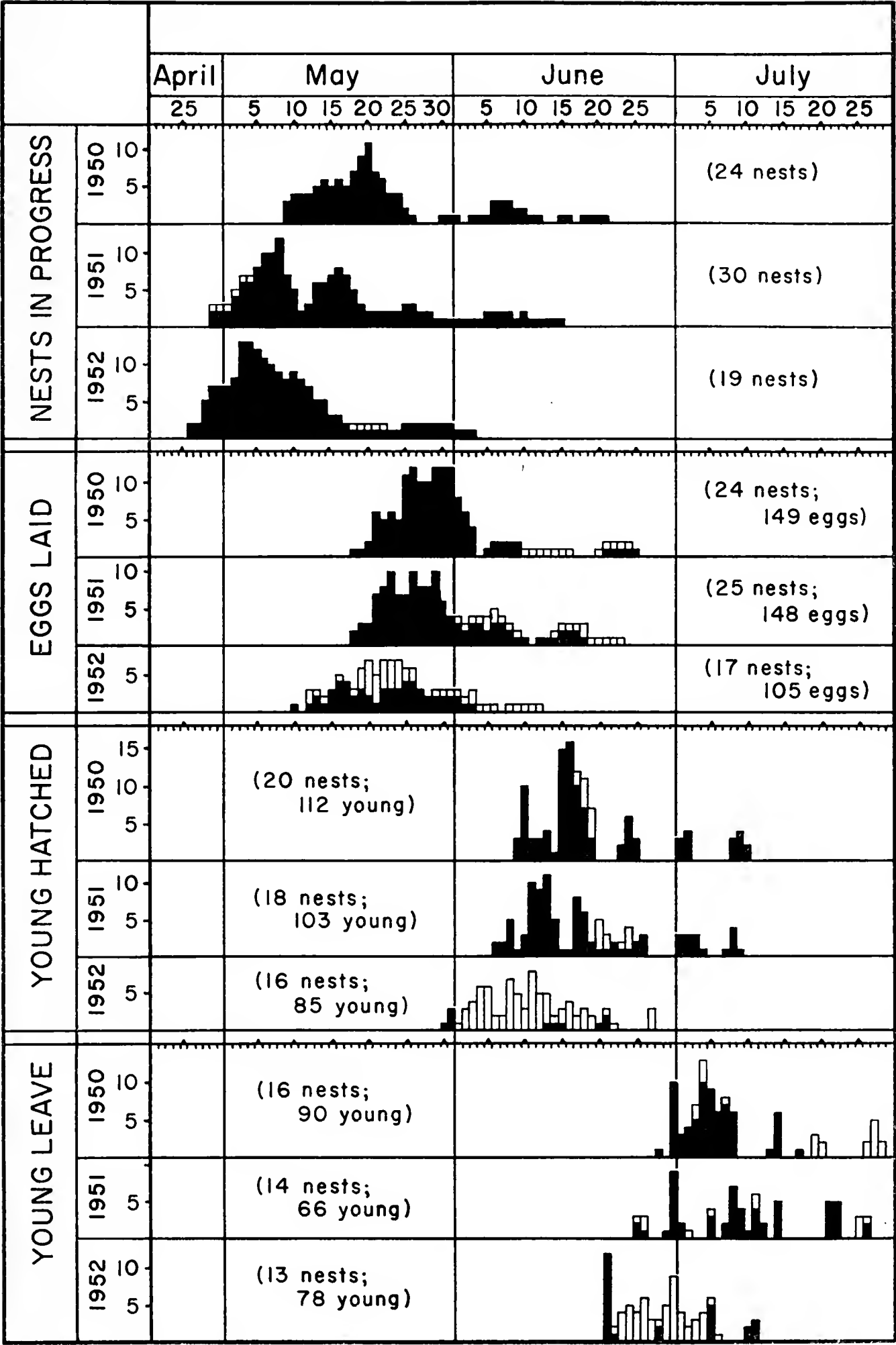


FIGURE 18. Dates of nest building, laying, hatching, and departure of young from nest, for the seasons of 1950, 1951, and 1952 at Ann Arbor. Black bars indicate dates fixed by positive observation; open bars indicate approximate dates established by inference from those known.

such times they might have been delayed in arrival, retreated temporarily to more favorable areas, or perished from hunger or exposure. Since it is not clear, from my very localized observations, to what extent the degree of activity reflected the true numbers present in the area, I have thought it best not to deal with arrival as such.

Nest building. When building started, an index to the amount of breeding activity was afforded by a daily count of nests currently under construction. Information so obtained during the three seasons is plotted in Figure 18. The earliest and the average dates seem particularly significant, and these are summarized in Table 11, the figures being based directly on data from the graphs.

TABLE 11
YEARLY PEAKS AND EXTREME DATES
FOR STAGES IN THE ROUGH-WING NESTING CYCLE

Stage in Cycle		1950	1951	1952	Three-year Average
Nest Building	Earliest	May 9	April 29	April 26	May 15
	Latest	June 21	June 15	June 3	
	Average	May 23	May 15	May 9	
Egg Laying	Earliest	May 18	May 18	May 10	May 29
	Latest	June 25	June 23*	June 12*	
	Average	May 31	May 31	May 24	
Hatching	Earliest	June 9	June 6	May 30	June 16
	Latest	July 10	July 9	June 27*	
	Average	June 19	June 18	June 10	
Young Leave Nest	Earliest	June 28	June 25	June 21	July 5
	Latest	July 28*	July 26	July 11	
	Average	July 8	July 10	June 28	

* Approximate dates, in these cases, represent extremes.

Egg laying. That the time of egg laying has fluctuated materially, and independently of that of building, is shown in Figure 18, and in Table 11. In 1951, laying began no earlier than it did in 1950, though nest building was found in progress much earlier. In 1952, both building and laying were advanced; laying started 8 days earlier than in the two preceding seasons and, although it reached a peak much more slowly, appears to have averaged as much as a week earlier. Less yearly fluctuation is shown in laying than in building.

Hatching. The peak of hatching for each season follows the peak of laying by a nearly uniform interval of some 17 to 19 days. This interval would be related to the sizes of the clutches concerned, lapses in laying, and relative times at which incubation began, and would be affected by any differential egg mortality that occurred. Still, for all practical purposes, the hatching dates may be considered as directly dependent upon the laying dates.

Nest leaving. The peak dates for nest leaving, in relation to those for hatching, are of course a direct reflection of the nestling periods, except for modifications brought about by mortality. No yearly variations in nestling periods have been detected, such as might result from changed environmental influences; and hatching and nest-leaving dates are separated by approximately the expected intervals.

RELATION TO WEATHER CONDITIONS

The processes of nest building and of egg laying, which have been shown to vary somewhat independently in timing, thus represent successive responses to stages in the Rough-wing's physiological cycle, each of which should be correlated with observable climatic conditions in the area.

Considering the relatively long period that building of a single nest may require, and the differences in the times at which various ones were started, it seems improbable that the building impulse is entirely dependent upon any one factor. The threshold, perhaps, is reached by proper combinations of temperature, humidity, and hours of sunlight, along with freedom from the inhibiting effects of precipitation and wind. That a rather delicate balance exists is evident to anyone watching the birds' intermittent activity.

Kuerzi (1941: 21-23) was able to show in his study of Tree Swallows, for which the normal time required for egg development was determined as about 6 or 7 days, that periods of adequate warmth and sunshine had each year preceded, by about this interval, the onset of laying in the colony. He evolved a tentative formula for the threshold of laying, in terms of temperature during those periods. I can select warm and clear periods, for each of the three years 1950-52, which coincided with some of the flurries of nest building and which preceded the starting of some early clutches by about a week. Undoubtedly a threshold of laying is the fundamental determinant of the schedule of all subsequent steps in the breeding cycle. However, the "start of general laying" (Kuerzi, *loc. cit.*) for the Rough-wings is a more protracted affair not closely related to the earliest laying. As is the case for nest-building dates, I am unable to find any satisfactory basis for more than general correlations.

Season of 1950. An unseasonably cold and wet period prevailed, in 1950, throughout the latter part of April. Although Rough-wings had been present in the study area at least by April 22, the few mild days interspersed thereafter were not sufficient to bring about any building activities. An abrupt change in weather took place, and the first week of May was generally mild and pleasant, except for considerable wind. May 8 was clear, but cooler. On the next day the first nests were begun (Figure 18), in spite of intermittent showers. May 10 was cool; but from then on there was a warming trend, and the rest of the month continued warm and pleasant, except for periodic rainstorms, mostly at night. Nest building continued and increased. When laying began, on May 18, favorable weather had seemingly continued for at least a week. The peak of laying, however, was not reached for another week, and it continued into early June.

Season of 1951. In 1951, it remained mostly cool, with some wind and rain, until about April 25; after this date the weather warmed, and continued unseasonably warm through about May 4. The Rough-wings began nest building the last two days of April, and through the first week of May nest building spread rapidly. Slightly cooler and breezy weather May 5 and May 6 did not greatly interfere with the activity; and during the three warmer days that followed a few nests were almost or quite completed. However, no eggs had been laid. The afternoon of May 10 and all day May 11 there was almost continuous cool rain, and activity of the birds was brought to a standstill. On each of the two days a number of individuals were found huddled together in holes, and an adult Rough-wing found dead in a hole probably perished about this time. Actual building had virtually ceased, and in few cases was it immediately resumed. At least one early nest was deserted, and in a few others long lags in the construction resulted. Several nests that had been previously completed were apparently neglected for a time. Beginning May 12, fair and warm weather returned, and conditions were generally favorable from that time on. Additional nests were begun and building of a few earlier ones was completed. The first egg was laid May 18; then laying rose rather rapidly to a peak, continued at a high rate until nearly the end of the month, and fell off gradually through the early part of June. These events emphasize the inhibiting effects that briefly adverse conditions can have, even when the prevailing trends have been such as to induce nest building and an approach to the threshold of laying.

Season of 1952. A cool spell near the middle of April, 1952, was followed by a prolonged and unseasonable warm one, which continued

almost unbroken through the first week of May. Nest building by the Rough-wings began April 26, and continued with increasing vigor. Several of the nests were abnormally long in the process of construction. Cool days from about May 8 did not immediately interfere with the birds' activities; and on May 10 the first egg was laid. This was not followed, however, by an immediate increase of laying. Predominantly cool weather, with some rain, continued through to May 16; and the period from May 18 to 26 was also comparatively cool and rainy. Egg laying continued; but its peak was probably not reached until about May 20. The principal difference between the seasons of 1951 and 1952 was that in the latter the stimulus of warm and sunny weather continued until a few birds had reached their thresholds of laying. Once begun, the clutches were completed. The cooler weather that followed was not sufficiently extreme to inhibit the breeding impulses seriously; and additional birds shortly began to lay. The successive stages of building and laying were permitted to follow at approximately their normal intervals, and the entire nesting season was thus advanced.

NESTING SUCCESS

In the course of my four seasons' field work there were 66 nests for which I have adequate data on laying, hatching, and fate of nestlings. In these nests a total of 403 eggs were laid. (This shows an average of only 6.1 eggs per nest, since at least 4 of the clutches were probably not complete when destroyed.) Eggs hatched, in 52 nests, numbered 293; this was a 73 per-cent hatching success, an average of about 4.4 young hatched per clutch laid, and an average initial brood size (for nests in which any eggs hatched) of about 5.6. A total of 246 young, fledged in 43 of the nests, are thought to have left successfully, these representing 61 per cent of the total eggs laid (the reproductive efficiency), and 84 per cent of the total nestlings hatched; thus an average of about 3.7 young were fledged per clutch laid, and the average final brood size (for successful nests) was about 5.7. In this sample, 65 per cent of the nests in which eggs were laid were successful in fledging young. Twenty-two ($33\frac{1}{3}$ per cent) were completely successful: that is, with fledged young equal in number to the eggs laid. Davis (1952) has furnished, along with a brief discussion of survival statistics, a series of very clear definitions. These have been followed, in principle, in the preparation of Table 12, in which I give totals and probabilities computed for the whole four-year period, for each separate year, and for the nests with larger and with smaller clutches.

TABLE 12
SUMMARY OF NESTING SUCCESS FOR SEASONS 1949-52

Nests, with Numbers and Per Cent Successful		Eggs		Hatching**			Fledging**			
		Laid	Per Nest	No.	P	Per Nest	No.	PfE	PfH	Per Nest
1949	In 2 nests, total	11	5.5	10	.91	5.0	6	.55	.60	3.0
	In 2 nests (100%) hatching young	11	...	"	.91	5.0	"
	In 1 nest (50%, 50%) fledging young	6	...	6	"	1.00	1.00	6.0
1950	In 24 nests, total	149	6.2	102	.68	4.2	92	.62	.90	3.8
	In 18 nests (75%) hatching young	115	...	"	.89	5.7	"
	In 16 nests (67%, 89%) fledging young	104	...	93	"	.88	.99	5.8
1951	In 24 nests, total	142	5.9	97	.68	4.0	72	.51	.74	3.0
	In 17 nests (71%) hatching young	105	...	"	.92	5.7	"
	In 13 nests (54%, 76%) fledging young	80	...	72	"	.90	1.00	5.5
1952	In 16 nests, total	101	6.3	84	.83	5.3	76	.75	.91	4.8
	In 15 nests (94%) hatching young	96	...	"	.88	5.6	"
	In 13 nests (81%, 87%) fledging young	85	...	78	"	.89	.97	5.8
Total, 4 Years	In 66 nests, total	403	6.1	293	.73	4.4	246	.61	.84	3.7
	In 52 nests (79%) hatching young	327	...	"	.90	5.6	"
	In 43 nests (65%, 83%) fledging young	275	...	249	"	.89	.99	5.7
Clutches of 6 or Less *	In 39 nests, total	222	5.7	155	.70	4.0	117	.53	.75	3.0
	In 31 nests (79%) hatching young	176	...	"	.88	5.0	"
	In 23 nests (59%, 74%) fledging young	131	...	118	"	.89	.99	5.1
Clutches of 7 or More	In 23 nests, total	165	7.2	138	.84	6.0	129	.78	.93	5.6
	In 21 nests (91%) hatching young	151	...	"	.91	6.6	"
	In 20 nests (87%, 95%) fledging young	144	...	131	"	.90	.98	6.4

* Data for 4 nests (16 eggs) omitted, because total clutch not laid, or in doubt, when nest destroyed.

** P - probability of hatching. PfE - probability of fledging from egg. PfH - probability of fledging from nestling.

PROBABILITIES

The figures in Table 12 are relatively consistent for the four years. While all the probabilities are comparatively high, the most strikingly so are those for the fledging of hatched young. In 1950 and in 1952, 90 per cent or more of all young survived to leave the nest. In successful nests, survival figures range from 98 to 100 per cent, being 99 per cent for the three years. In other words, except where entire broods were destroyed, nearly all nestlings survived. The reduced probability of fledging of nestlings in the 1951 season is largely attributable to loss of broods to weasels (as described beyond).

From a number of the nests here considered, I removed individual young for preservation. Rather than eliminate these nests from the analysis entirely, I have treated them as if all such young had remained, and have assumed that they would have shared the fate of the rest of the brood, an assumption justified by at least 99 per cent of the data.

Blake (1953: 108) points out the desirability of weighting statistics to allow for differential survival in large and small broods. Although I have not treated individual clutches, as he suggests, I did treat all nests with six or less eggs in the original clutch separately from those with clutches of seven or more. Most of the figures are higher for the nests with larger clutches, and the over-all reproductive efficiency is considerably so. Statistically, the difference is highly significant, the t value of about 5.05 being at the level of a very small fraction of a per cent (Snedecor, 1940: 57). However interesting this result may appear, the nature of the losses seems to preclude anything more than coincidence (but cf. Paynter, 1954: 102-103).

I am certain that there was never more than one nest per pair per season in which young were hatched. In at least half a dozen instances, however, nests were known or surmised to represent successive attempts by the same female or pair. Some of the averages "per pair" would therefore be slightly higher than those "per nest," if my data permitted determinations on this basis.

Comparisons with other studies. The only previous statistics on Rough-wing survival I have seen are those of Blake (1953: 108). For five nestings observed in Massachusetts, he reports probabilities "for hatching 0.75, for fledging from eggs 0.68 and for fledging from nestlings 1.00," figures which, like others in the paper, are very similar to some of mine.

The reproductive efficiency of other swallows seems to be moderately high, although subject to great fluctuation. Most studied has been the Tree Swallow, for which Allen and Nice (1952: 639-641) give compiled figures showing that "the average success of the five studies involving 3859 eggs was 59.6 per cent." For Tree Swallow nests

studied in Montana, Weydemeyer (1935: 216) gave figures indicating a tremendously high efficiency of about 93.7 per cent. But judging from the variable results of other studies (cf. Low, 1934: 29; Kuerzi, 1941: 36-39; Paynter, 1954: 49-51, 102-104; Winn, 1949), this was exceptional. Allen and Nice (1952: 636-639) summarize statistics for the nesting of the Purple Martin based on three studies. Allen's own investigations showed the lowest percentage of efficiency, 38.5; highest was the doubtful figure of 61.6%, based on the extensive but not precise records of Jacobs (1903: 14, etc.). These species and the Rough-wing are hole nesting, and might be expected to have relatively high reproductive efficiencies (Nice, 1957). The Barn Swallow nests in more exposed situations; and Wood (1930: 90) gave figures for the success of that species which indicate something over 54 per cent efficiency.

MORTALITY AND NEST FAILURE

In Table 13 is a summary of observed nesting *losses*, for the four seasons individually and for the entire period of the study. In all, 38 nests incurred some loss of eggs (total loss in 14 cases), and 12 nests some loss of young (total loss in 9 cases). These (6 of them losing both eggs and young), plus 7 deserted or destroyed before laying, make

TABLE 13
SUMMARY OF ROUGH-WING NESTING LOSSES AND OF ADULT MORTALITY
FOR FOUR SEASONS 1949-52

Years	Total Nests Treated	Nests Failed before Laying	Eggs Laid	Loss of Eggs				Loss of Young					Known Loss of Adults
				Nests		Eggs		Nests		Young			
				Any Loss	Complete Loss	Number	Per Cent	Any Loss	Complete Loss	Number	Per Cent of Lay	Per Cent of Hatch	
1949	2	0	11	1	0	1	9	1	1	4	36	40	0
1950	26	2	149	15	6	47	32	3	2	10	7	10	1
1951	29	5	142	13	7	45	32	4	4	25	18	26	2
1952	16	0	101	9	1	17	17	4	2	8	8	10	2
4-year Total	73	7	403	38*	14	110	27	12*	9	47	12	16	5

* See note below Table 14.

a total of 51 nests treated; 30 of them failed completely and 21 were partly successful. The total loss, 39 per cent ($= .39$ probability) is of course the probability of dying (q), and the quantity $(1 - q)$ equals p , the over-all probability of survival (Davis, 1952: 316-317). Also incorporated in Table 13 are such figures as I have on the mortality of adults on the breeding grounds.

DESTRUCTIVE FACTORS

In Table 14 I have broken down the four-season totals to show the relative effects of various agencies responsible for the losses, all percentages being of *eggs laid*. Certain factors require special comment.

Desertion. Although desertion may be but a secondary cause of nest failure, it is often difficult to assign any other. My activities and adverse weather have at times been contributing factors.

Slipping of eggs from nest. The construction and placement of the nest make the Rough-wing particularly liable to dislodge an occasional egg from the cup, presumably in the act of leaving. Three eggs were found pulled out into the passageways, and perhaps half a dozen others were presumably lost in the same way. In Nest 23, which was of unusually loose construction, two of the clutch were gradually pushed downward through the lining during incubation.

Failure to hatch. Table 14 shows that 19 eggs (4.7 per cent of those laid), belonging to 15 different clutches, failed to hatch. In a few instances some external agent (such as interference with incubation) may have contributed. Generally speaking, however, the eggs were all sterile or "addled," the latter term being admittedly of rather loose application. In the majority of cases gross inspection in the field showed no indication of embryonic development. Assuming that a similar proportion would have been found among the eggs that were otherwise lost or damaged, the real incidence of this hatching failure must have been something like 6.1 per cent (one egg in 16). The occurrence appeared to be largely random, usually a single egg in about every second or third clutch; and I was unable to detect any correlation with sequence of laying, date of laying, start of incubation, or size of clutch.

The summary by Allen and Nice (1952: 646) indicates that infertile and addled eggs are of extremely irregular occurrence in the case of the Purple Martin. Under favorable conditions the percentage was very low, "only three eggs . . . out of 79 laid." High incidence was possibly attributable in one case to early laying, and in another (as paraphrased from Widmann, 1922: 6) to "irregularities of incubation with the first-laid eggs." If I correctly interpret Kuerzi's data (1941: 37-38) for the Tree Swallow, he found that nearly 20 per cent of eggs not destroyed still failed to hatch.

TABLE 14
CAUSES OF MORTALITY, DESTRUCTION, AND LOSS
DURING FOUR SEASONS, 1949-52^a

Agencies	Nests Failed before Laying	Loss of Eggs				Loss of Young				Total Nest Loss				Known Loss of Adults
		Nests		Eggs		Nests		Young		Nests		Eggs and Young		
		Any Loss	Complete Loss	Number	Per Cent	Any Loss	Complete Loss	Number	Per Cent of Lay	Any Loss	Complete Loss	Number	Per Cent of Lay	
Desertion	5	2	2	8	2.0	7	7	8	2.0	...
Breakage	...	2	...	3	.7	2	...	3	.7	...
Slipping from nest	...	4	...	5	1.2	4	...	5	1.2	...
Failure to hatch	...	15	...	19	4.7	15	...	19	4.7	...
Action of elements	...	2	2	9	2.2	1	1	5	1.2	3	3	14	3.5	1 ?
Human disturbance (excl. my own)	...	2	2	12	3.0	3	3	9	2.2	5	5	21	5.2	...
My accidental damage	...	2	...	2	.5	1	...	1	.2	3	...	3	.7	...
Weasels	...	2	2	9	2.2	4	4	24	6.0	6	6	33	8.2	2
Other predators	...	1	1	6	1.5	1	1	6	1.5	...
Disturbance by other animals	1	1	1	6	1.5	2	2	6	1.5	...
Undetermined	1	10	4	31	7.7	4	1	8	2.0	14 ^b	6	39	9.7	2
Total Loss	7	38 ^b	14	110	27	12 ^b	9	47	12	51 ^b	30	157	39	5

^a Percentages based on total of 403 eggs laid.

^b The total nests incurring some loss subsequent to laying, under any given heading, are not necessarily the sum of those in component categories, for successive and unrelated losses frequently took place in the same nest.

Action of the elements. In two cases, eggs were completely buried after washing away of banks by heavy rain. In a third (Nest 38) the young, exposed to undue extremes of temperature, ultimately perished. Probably, during my study as a whole, the partial protection afforded by the use of my nest tubes rendered this factor less destructive than it otherwise would have been. Dingle (1942: 430) suggested that "probably the greatest cause of destruction to eggs and young [of the Rough-wing] is the flooding of the burrows by spring tides and river freshets." He quotes Wayne (1910: 141), who describes frequent losses of eggs and young from this source in South Carolina.

The susceptibility of adult swallows to inclement weather is a well-established fact, particularly for those species which are early migrants and frequently face rigorous conditions at the beginning of the season. Although specific records are lacking, considerable mortality of adult Rough-wings must result from time to time, as is indicated by observations I have already discussed.

Predation by weasels. Worthy of separate consideration is the Long-tail Weasel (*Mustela frenata*), which during my study caused greater damage than any other known factor, taking the contents of six nests, equivalent to 8.2 per cent of the eggs laid, and at least two adult female birds. This was in addition to damage to adjacent Bank Swallow colonies, which I did not even attempt to estimate, but which I know was extensive. A small male weasel, captured in the tube containing my Nest 19, had killed and eaten the female Rough-wing, and eaten all of the four or five eggs (the clutch still incomplete) except part of one. It had remained in the nest chamber to consume the bird and the eggs, and perhaps to rest during the day. I similarly captured two other individuals, both young of the year and quite probably litter mates, at Nest 76, which had contained half-fledged young Rough-wings. At dusk on June 29, 1951, David F. Parmelee and I saw a weasel that was causing a great disturbance among the Bank Swallows of a colony in Pit "A". It ran with apparent ease over the sloping sand bank, and entered at least five successive burrows before it saw us and disappeared.

A great many Bank Swallow nests, situated high on fresh-cut vertical sand banks, would almost surely be out of the reach of weasels, agile as the creatures are. The Rough-wing's regular use of older burrows, on less precipitous slopes, however, and particularly of such sites as my artificial tubes, makes it especially vulnerable.

Contrary to the experience of Elliott (1946), I found that in every case the Longtail Weasel devoured its prey almost completely. Characteristically, there was nothing left but a few fragments of shell, some of the larger quills bitten off close to the base, or sometimes a bit of bill or a piece of wing. Generally there was enough of the

ropy excrement, deposited in the passageway or below the entrance, to identify the predator and to give evidence of the considerable time it had spent at the site.

Other predation or disturbance. One nest (73b) was destroyed by a predator never certainly identified. Another (89), built in a very shallow burrow, was destroyed by Belted Kingfishers, before any eggs had been laid. The kingfishers took over the site and deepened the burrow greatly, throwing out the completed Rough-wing nest in the process. Nest 69 was lost through the curious circumstance of a toad (a medium-sized specimen of *Bufo americanus*) resting in the passageway or on the nest, probably for two days, so that incubation could not be begun, and desertion followed.

Unknown causes. In a number of cases, circumstances of losses were obscure. Occasionally, for example, a single egg or nestling simply disappeared between successive inspections, or was unaccounted for when a brood was finally examined. Eggs from two nests vanished without a trace. Below another nest, the remains of four Rough-wing eggs (and not far away two of Bank Swallows), bore double punctures made by the mandibles of a small bird. The outlines, however, were not sufficiently sharp for identification. House Sparrows were in the neighborhood, and might be suspected; Allen and Nice (1952: 642-643), for example, cite references to their destruction of Purple Martin eggs. Dawson (1898) alludes to the probable dispossessing of Rough-wings by House Sparrows nesting in shale cliffs in Ohio; and Paynter (1927) describes their destruction of Barn Swallow eggs. Two adult male Rough-wings were picked up dead below nest tubes: one bore no sign of injury, while the other may have received a blow on the back of the head.

Literature. Very little definite information has been published on mortality of the Rough-winged Swallow, or upon its enemies. Bailey writes (1913: 261-262) that "the mortality in this section [Virginia] is great, their chief enemy being the black snake." In my study area this predator was certainly not important, although in a few instances the possibility of loss to snakes could not be ruled out. Dingle also suggests (1942: 431) that on the South Atlantic coast "the common sand crab (*Ocypode albicans*) might, to a limited extent, prey on eggs and nestlings of the rough-wing." Snyder (1950) has presented a remarkable account of a collision of two Rough-wings in mid-air, which caused the death of one. Starrett (1938: 195) lists five Rough-wings as highway casualties, near Peoria, Illinois, in 1937. Young Bank Swallows have been described (Stoner, 1936: 215; Beyer, 1938: 132-133) as commonly falling from the burrows when partly fledged. I have often found young Bank Swallows of various ages at the foot of banks; and one young Rough-wing about two weeks old was found dead.

Among Tree Swallows, according to Low (1933: 87), an important loss of young was due to "crowding by their older siblings in the nest when they were still very young." It seems particularly significant that, despite the generally large brood sizes and the frequency of wide age disparity within a brood, I found not a single death that could be attributed to this factor.

CONTACTS INVOLVING OTHER SPECIES

Various contacts not shown to contribute directly to the mortality or nest losses of Rough-winged Swallows still have a potential bearing upon their success, or bear in some special way upon their behavior.

PARASITES

Among all of the broods observed and handled, I recorded no deaths, and only one or two cases of temporary weakness, that could reasonably be attributed to the presence of internal parasites in the young. External parasites were of very infrequent occurrence.

Blood-sucking fly larvae. From young of the second Rough-wing brood that I handled (Nest 11, 1949) I took a number of medium-sized (approximately 1 cm. long), purplish, dipterous larvae. Never again during my study did I find any evidence of such infestation, and unfortunately the specimens were not sufficiently well preserved to be identified. It is presumed that they were a species of *Apaulina* [= *Protocalliphora*]. Parasites of this genus have been reported as destructive to nestling Purple Martins (Allen and Nice, 1952: 646-647), Bank Swallows (Stoner, 1936: 216-219; Lincoln, 1931), Barn Swallows (Woods, 1926; Lincoln, *loc. cit.*), and Tree Swallows (Johnson, 1932: 26-28), along with a great variety of other species. It is perhaps significant that Nest 11 was one of the latest which I studied intensively. Others have remarked that only late broods were infested by *Apaulina* (Allen and Nice, *loc. cit.*), or at least that they suffered most heavily (Stoner, *loc. cit.*).

Fleas. A single flea (unidentified) was seen to jump from a member of the late brood mentioned above (Nest 11). Otherwise I saw no fleas directly upon the birds or in their nests. Late in the season, however, I often saw numerous fleas clustered about the entrances of Bank Swallow burrows. In one case (Nest 46) I estimated about forty of these insects at the mouth of a burrow in which was a two-thirds-fledged Rough-wing brood; this burrow had previously been used by Bank Swallows and other Bank Swallow nests were, or had been, closely adjacent. Rothschild and Clay (1952: 80) discuss the habits of the Old World Sand Martin Flea (*Ceratophyllus styx*); and

also (p. 86) remark upon the evolution of its American counterpart, *C. riparius* of the Bank Swallow.

Mites. On a very few occasions, while handling nestlings or examining empty nests, I noted minute pale-brownish mites. Reported by Peters (1936: 19) from the Rough-winged Swallow are two mites: *Atricholaelaps* sp., from Virginia; and *Liponyssus sylviarum*, from Maryland. The latter, the Northern Fowl Mite, "was found on 22 species" (*op. cit.*: 10), including the Bank Swallow and Barn Swallow.

AMPHIBIANS AND REPTILES

Frogs and toads. I have described the loss of a clutch of eggs when a toad took refuge in the nest cavity, and other observations suggest that this was by no means a unique occurrence. Previously, a medium-sized Bullfrog (*Rana catesbeiana*) had been found backed into the entrance of the same tube, then containing Nest 28. This tube, located near the top of an unusually high (estimated about fifty feet) and steep red-clay bank, seemed particularly difficult of access for these animals. In other tubes, unoccupied by swallows, I found toads on at least four occasions, and once a large Leopard Frog (*Rana pipiens*). In any sort of burrow with a relatively narrow entrance a potential danger to nesting swallows from this general source would exist. Skutch (1960: 271) mentions the presence of toads in burrows occupied by Rough-wings in Guatemala.

Snakes. On June 15, 1950, I found a garter snake (*Thamnophis* sp.) about 18 inches long, part way up a bank some five feet below Rough-wing Nest 39, which was in a small Bank Swallow colony. I watched the snake through binoculars, as it made repeated attempts to climb a steeper section of the sand bank toward a group of burrows. The incident gave no evidence of predation; but it did show me how such a potential predator, taking advantage of all irregularities, could work its way up a fairly steep bank of soft sand.

MAMMALS

Badger. One Rough-wing nest was destroyed and a number of Bank Swallow burrows dug out and emptied, by some medium-sized mammal. Holes dug at these sites were up to eight inches in diameter. Very large and deep claw marks, sometimes reaching as much as three feet up a vertical face, could hardly have been made by anything but a badger (*Taxidea taxus*).

Weasel. There were a few cases, during my inspections of the tubes in winter or very early spring, in which it was evident from nesting materials, characteristic odor, and other signs, that weasels of some species had used the nest chambers for winter quarters. Extensive nest predation has been discussed previously.

Woodchuck. On numerous occasions, I saw woodchucks (*Marmota monax*) in and around the pits. Many tracks and diggings found from time to time probably belonged to this species. At one hole in a bank (in Pit "A") where I saw a woodchuck, I also saw Rough-wings several times investigating for possible nesting sites. On one occasion a woodchuck looking out of this burrow had a group of six Rough-wings circling close, calling, and diving at it. At another time, I watched about four Rough-wings, along with a larger number of Bank Swallows, circling close to a woodchuck, which was walking along the upper rim of Pit "C" not far above nests of both species. The birds called, and several made sporadic dives at the passing animal.

Thirteen-lined Ground Squirrel. *Citellus tridecemlineatus* was a common species in the fields adjacent to the gravel pits, and occasionally came down into the pits. I found a large individual in the chamber of Nest 98 (in Tube 1), which at the time contained an incomplete clutch of eggs. One of the eggs was broken; but it appeared that none of it had been eaten. Later, another egg was broken, and all were pushed down considerably, suggesting that the same rodent had returned to the nest. On the first occasion, two Rough-wings were seen circling near, but without a great show of excitement. Earlier, June 26, 1949, I had seen a single Rough-wing, probably a male, make four passes in quick succession at a ground squirrel on a road some fifty yards from any nest, and pursue it closely until it scuttled off into the weeds.

Other rodents. I saw two Rough-wings pursuing a chipmunk (*Tamias striatus*), several yards below Nest 65, diving repeatedly at it as it ran past on the bank.

Many times I found, during the late summer, winter, and spring, that mice had carried nesting material into my tubes, and often completely filled the chambers. Extreme accumulations of this mouse-nest material, if I did not remove it, made the sites unacceptable to Rough-wings. All mice I captured or observed were White-footed Mice (*Peromyscus leucopus*).

RELATIONS WITH OTHER BIRDS

Bank Swallow. The Rough-wing nests in my area were seldom more than a moment's flight from groups or sizable colonies of nesting Bank Swallows. Even so, under many circumstances the two species were indifferent to one another. Early in the season, when both were selecting nest sites and often intermingled about the freshly dug holes, displays of mild antagonism, and occasional brief pursuits, were frequently seen to involve both species. Although the Rough-wing was more frequently the aggressor, it was not invariably so. I saw no

evidence that Bank Swallows were forcibly evicted from burrows; rather the Rough-wings seemed to remain in the vicinity, perching, hovering, circling about, and examining holes, until some suitable burrow was vacated. However, Eliot (1932: 102) remarks upon a pair "at a small Bank Swallow colony, apparently trying to oust the owners of one hole there." The possibility of such behavior remains to be thoroughly investigated. In any event, the Rough-wings were to a considerable extent dependent for nest sites upon the excavations of the Bank Swallows, which always dig, or at least begin, many more burrows than they use for nesting (cf. Stoner, 1936: 181). Sites selected were frequently, though by no means always, among smaller groups of holes or on the periphery of the larger colonies. As the nesting season advanced, antagonism between the species was less evident (as it was between individuals), with only now and then a threat or a momentary pursuit, close to a nest of one or the other species. I observed Rough-wing nests located less than a foot from active nests of Bank Swallows, with no evidence of conflict.

Occasionally I noted Rough-wings aggressively pursuing young Bank Swallows on their early flights from the nests, as they did young of their own species, and as adult Bank Swallows themselves were often seen to do. On three occasions, twice in Nest 82 and once in Nest 25, I found Bank Swallow fledglings that had taken refuge in nests with broods of young Rough-wings slightly behind them in development; there was no evidence that these interlopers caused any animosity on the part of parents or young.

Belted Kingfisher. Next to those of the Bank Swallow, the burrows of this species were the natural sites most commonly used by Rough-wings in the areas I studied. Kingfisher holes regularly last through the winter, and provide acceptable sites the following spring. In addition, as pointed out by Blake (1953: 107) in regard to a Massachusetts locality, the kingfishers often make several attempts before completing a burrow that meets their needs, the unfinished tunnels being quite adequate for the Rough-wing. Generally speaking, I have observed very little direct contact between the two species. The destruction of one Rough-wing nest described previously was presumably quite incidental to the kingfishers' deepening of the burrow for their own use.

House Sparrow. As a possible predator, this species has already been mentioned. So far as my observations were concerned, however, the House Sparrows in the area were merely taking advantage, as were the Rough-wings themselves, of the numerous available nesting sites; and in that way a certain amount of direct competition may have come about. I had House Sparrow nests, both of which successfully fledged young, in Tube 13 in 1951 and in 1952. Both years several Rough-wings were seen investigating the site about the time

the sparrows took possession, but no direct conflict was noted. A male Rough-wing was picked up dead a few feet below this tube, after the 1951 nest had been completed. In each sizable Bank Swallow colony that I investigated to any extent, I found one or more holes taken over by this species. Two Rough-wing nests (85 and 88) were built directly on top of abandoned House Sparrow nests.

GREGARIOUSNESS

Although the Rough-wing is not fundamentally to be considered as a colonial species, it shows some of the gregarious tendencies that characterize the Hirundinidae as a group. Individuals not engaged in actual territorial or sexual conflicts show a degree of tolerance that amounts almost to sociability. They commonly fly about, perch, and perform aerial maneuvers in groups of from three to a dozen or more, in a manner that most strongly suggests a form of play. Extra birds keep appearing at nesting sites, from the time the site is first examined until the young are leaving the nest. Often their presence arouses no evident animosity, and I can only interpret the behavior, in a great many cases, as a sort of casual "visiting." Occasionally, a bird actually enters a hole that is not its own. A marked female with partly grown young of her own was seen to disappear for about five seconds into a neighboring nest, where there were six eggs about ready to hatch and both adults were temporarily absent.

Gatherings of considerable groups of Rough-wings (often mingled with Bank Swallows as well) take place in response to external disturbances. Generally there are only one or two birds calling (the pair at whose nest the disturbance occurs?); but the others circle, dive, and pursue one another, fresh birds continuing to join, until the whole group rather suddenly disbands. I have seen similar behavior on the part of Bank Swallows when a weasel was visiting the holes, and at other times when the focus of interest was not apparent. It must not be quite analogous to the "towering" described by Kuerzi (1941: 11-12) for Tree Swallows. The latter is said to be unrelated to external disturbance, and to involve all the birds in the colony, the reaction to an intruder being more localized and directly aggressive. While, with the Rough-wing, the gatherings usually seem motivated primarily by curiosity, the habit might under certain conditions serve as a sort of communal defensive mechanism.

Another indication, at least, of a group reaction is the immediate response of Rough-wings to an alarm note of another of their kind. On three or four occasions I have chanced to be watching two or three perched Rough-wings, when a single such alarm note was heard from another individual a considerable distance away, and have seen them fly up instantaneously.

POPULATION DYNAMICS

Most of what I learned of the population structure and of individual movements was incidental to subjects that have been already considered. Published studies of other, generally much more strongly colonial species, in which extensive banding and marking data have been analyzed (e.g., Bergstrom, 1951; Stoner, 1925-28, 1936, 1937, etc.; Mason, 1953; Emlen, 1952, 1954; Mayhew, 1958; Allen and Nice, 1952; Chapman, 1935, 1939; Kuerzi, 1941; Low, 1934; and Boyd, 1936), have been highly instructive — but in this connection a Rough-wing population such as the one I studied is scarcely comparable. Certain miscellaneous evidence may, however, be useful if brought together.

Size of the population. In 1950, I estimated that there were approximately 50 (between 45 and 54) breeding adults within the area of my principal study (see map, Figure 1). Results of my 1951 estimates were almost exactly the same, about 47 to 50 adults having been involved in observed nestings. During each season there may have been a small number of nests that I failed to find. In both seasons also, there was evidence that a small nonbreeding population was present; in part this may have comprised individuals that failed early in nesting attempts and did not renest. In 1952 the indications were that the breeding population remained on a level comparable with that of the two previous years.

Breeding age and dispersion. In 1951, I caught the female of Nest 92 (north of Pit "A"), which had been banded the previous summer as a nestling in Nest 27 (in Pit "A"). In addition to demonstrating conclusively the first-year breeding of an individual, this provides one example of the return of a young bird to within six hundred yards of the point at which it was raised. Perhaps more significant, however, is that no other banded young were retaken as locally breeding adults, which would seem to indicate a considerable dispersion into surrounding areas.

A female I banded (50-11129) at her nest in 1951 was retaken in 1952 nesting in the same place (Tube 12). In 1951 this individual was at least one, and (since my notes made no mention of immature plumage characters) probably at least two years old. In 1952, therefore, it was a vigorous breeding bird (laying a clutch of seven eggs, all but one of which hatched), at two, and probably three years of age. Another female was banded (50-11123) in 1951 and retaken in 1952. Apparently fully adult in 1951, it was probably at least three years old in 1952, when it laid a clutch of six eggs, five of which hatched. Whether it nested both years in the same pit, or possibly in the same spot, is not known. A record in the Fish and Wildlife Service files (A. J. Duvall, letter) indicates a minimum age of almost four

years for a Rough-wing banded in April, 1936, by D. S. King in Arizona, and retaken at the same point in March, 1940.

Gillespie's homing experiments (1934: 43-44) are of interest. One member (probably the male) of a nesting pair of Rough-wings at Glenolden, Pennsylvania, was marked and released, on successive trials, from points 4 miles northwest, 7 miles south, and 32.8 miles south. Each time it returned to the nest within a few hours.

The longevity of the Rough-wing might be expected to be at least equal to that of the Bank Swallow. For the latter, Stoner (1938: 177) calculated a probable life span of "from two to three years," citing the small percentage of four-year-old banded birds, and but one individual known to be six years of age. Later the same author (Stoner and Stoner, 1942) published a note on a single seven-year-old Bank Swallow. Mason (1943a) reports an eight-year-old Barn Swallow and (1943b) a six-year-old Tree Swallow. Other swallow species studied have been shown (e.g., Stoner, 1936: 229; Mason, 1953: 98-99; Keurzi, 1941: 25-26) to breed regularly in their first year.

Brood size. As already indicated, the average number of young I found was 5.6 to 5.7 per brood. The greatest number I have yet seen has been 7, each clutch of 8 eggs having had less than complete hatching success. However, Blanchard and Nelson (Wood, 1951: 289) found "a nest with 8 newly hatched young" at Douglas Lake, Cheboygan County, Michigan. If, as I found, about 65 per cent of the clutches laid produce young, each breeding pair of adults could be expected (with second attempts) to raise an average of considerably more than 3.7 (and probably somewhat over 4) young per season.

WING SERRATIONS

Though the peculiar serration of the outer (ninth) primary of *Stelgidopteryx* has been commented upon from the time of the earliest descriptions, its biological significance remains a fascinating enigma.

STRUCTURE

Almost every general account has included some brief description of the "rough" primary, but surprisingly little close study seems to have been given it. Simple illustrations are frequently given, as for example by Audubon (1838: 595), Chapman (1912: 420), Ridgway (1904, Pl. 2) and Roberts (1932: 44). Descriptions generally attribute the serrations only to the adult male (Ridgway, *op. cit.*: 57), or state that they are absent in the juvenal plumage and usually less distinct in the adult female (Dwight, 1900: 230-231). A rather detailed note by Steinbacher (1931) compares the primary serrations

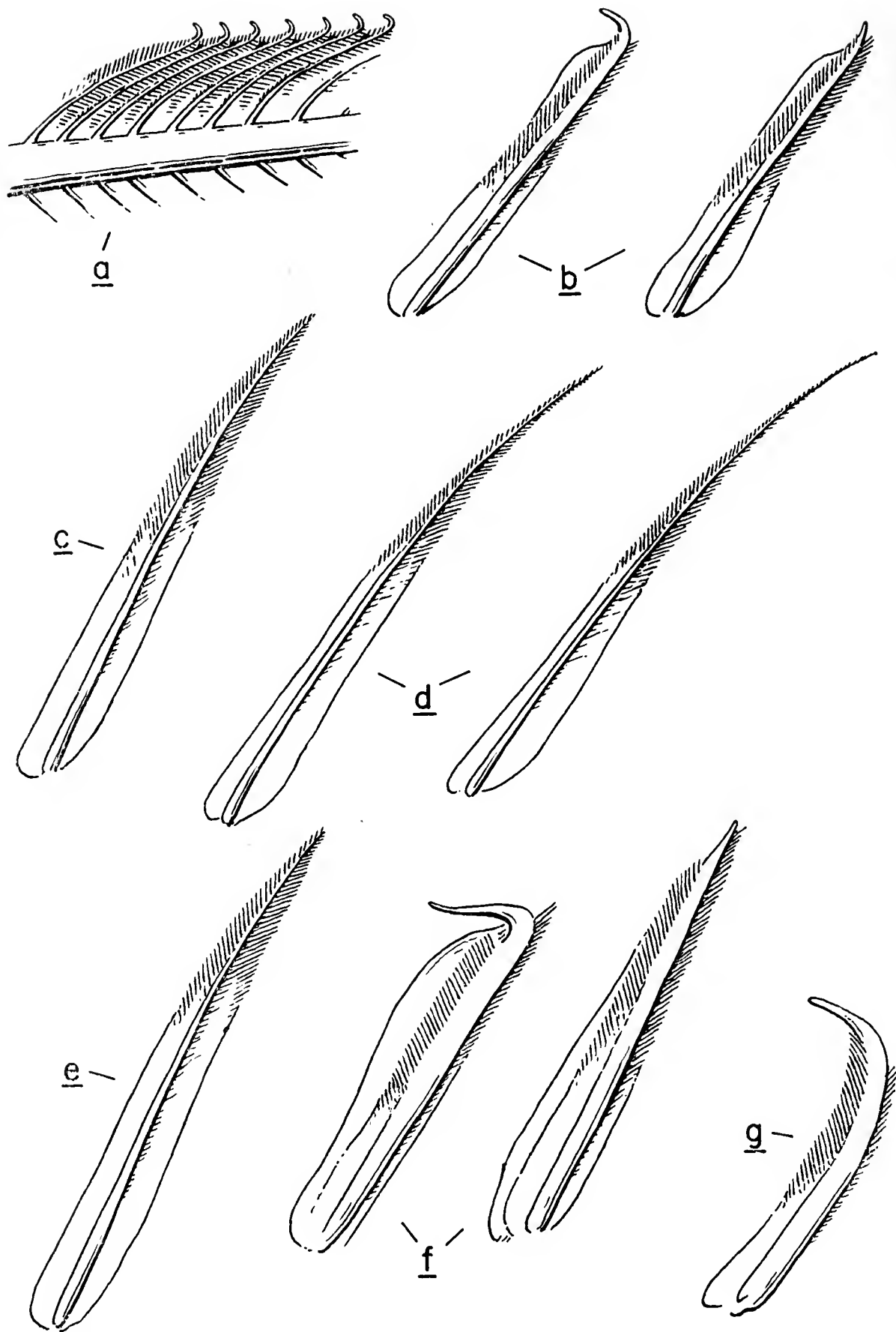


FIGURE 19. Structure of the barbs of the outer primary in several species, to show relative development or nondevelopment of hooklets. In *a* is illustrated a short segment of the outer web of the right outer primary of a Rough-winged Swallow (dorsal view), showing position of hooklets. Single barbs shown are from: *b*, adult Rough-winged Swallows (left, male; right, female); *c*, a male Rough-wing in juvenal plumage; *d*, Bank Swallows (left, juvenal plumage; right, adult); *e*, a Cave Swallow (*Petrochelidon fulva*, male); *f*, the African Rough-wing *Psalidoprocne petiti* (left, adult male; right, adult female); and *g*, a Sharp-bill, *Oxyruncus cristatus* (adult male). (All barbs are from the right wing, and drawn to show dorsal or anterodorsal aspects.)

of *Stelgidopteryx* with those possessed by the African Rough-winged Swallows of the genus *Psalidoprocne*. The structure of the modified barbs in the male of the former genus is well described and figured; it is erroneously implied, however, that the female of *Stelgidopteryx* exhibits no modification whatever.

It is not my purpose to present a detailed morphological study. Certain comparisons, however, are of interest; and sketches in Figure 19 will serve to illustrate important points. In *a* is shown the general arrangement of well-developed hooklets in a *Stelgidopteryx* male. The serration extends along the whole length of the exposed web, growing weaker towards the tip, where for about the distal ten millimeters it is essentially absent. In *b* a single barb is further enlarged to show the relation of the barbules to the naked hooked tip. Adjacent is shown a corresponding barb from an adult female. The entire barb is short and stout, as in the case of the male, and the tip prolonged into a definite naked point. These points are in many individuals clearly evident as producing a sawlike edge to the primary; but the essential sexual difference is that in the female they normally are *little or not at all recurved*. I have found one apparent exception to this, in a specimen (U.M.M.Z. No. 110864) labeled as a female and having measurements indicating it was correctly sexed. In both sexes there is considerable variation (due in part, certainly, to age) in the degree of development. In Figure 19*c* is shown a barb from the outer primary of a juvenile male. This is much longer than adult barbs, and unmodified. For comparison I have shown, in *d* and *e*, some barbs from the outer primaries of two other swallow species. In the Bank Swallow, even the juvenal feather has conspicuously longer and more pointed barbs than in the Rough-wing, and those from an adult feather are extremely attenuate. In the Cave Swallow (*Petrochelidon fulva*) the barbs, while long, are broad and heavy, so as to approach the condition in the young Rough-wing.

The serrations found in *Stelgidopteryx* are not quite unique. In addition to characterizing also the several African species of *Psalidoprocne*, a similar structure is found in the Neotropical *Oxyruncus*, the Sharpbill, sole member of the family Oxyruncidae. Although Steinbacher (1931: 72) has figured modified barbs of both sexes of *Psalidoprocne*, I have included (Figure 19, *f*) sketches based on specimens of *P. petiti* that I examined. It is seen that the modification, while similar to that in *Stelgidopteryx*, is even more extreme, and differs in details. Again, the barbs of the female are distinctly modified, but straight. In *g* I have indicated the condition, well developed, in a male of *Oxyruncus cristatus* in the U.M.M.Z. collection. In another male specimen (immature if correctly sexed) the hooklets were much less pronounced, and in a female they were barely discernible.

It is surprising to read that Ridgway (1907: 333) found "the alleged serration . . . to be very indistinct in all specimens examined." Sick (1937: 306) has commented upon the parallelism shown by the forms I have mentioned, and relates all of these morphologically to certain modifications he describes (*op. cit.*: 260, 304-306) for Birds of Paradise of the genera *Paradigalla* and *Ptilorhis* (*Craspedophora*).

FUNCTION

No treatment of the Rough-wing's biology should omit some speculation as to the possible function of these rows of minute hooklets. A suggestion by Coues (1927: 356) that they "assist the birds in crawling into their holes, and in clinging to vertical or hanging surfaces," while repeated by a few other writers, is not very convincing. Dawson (1903: 282) aptly remarked in this connection that the hooklets could not be for clinging "unless, indeed, it is head downward—a habit which, so far as I am aware, has never been observed." He goes on to suggest, somewhat facetiously, that the roughened wings might be applied to the sides of the burrow to prevent forcible removal of the bird. No such behavior was ever noted in any of the birds handled—and the male is scarcely ever *in* the burrow. The most carefully thought-out theory I have seen advanced was that (proposed by Stresemann) which prompted the article by Steinbacher (1931) already cited. It is there suggested that the serrations in both *Stelgidopteryx* and *Psalidoprocne* form a clasping structure for copulatory purposes; and it is explained in detail just how the hooklets would operate, caught firmly in the plumage of the female, to prevent the male's slipping forward or sideways, while his feet prevented his slipping backward. Mating is supposed to take place in the confined space of a burrow. This proposition cannot at present be positively refuted. On the other hand, there is no evidence that copulation actually takes place as described. Steinbacher himself raises the question as to why no other swallows, such as the hole-nesting Bank Swallow, have developed similar habits and structures. Why a few species, among all birds, should benefit from such a mechanism, is difficult to imagine.

As a matter of pure speculation, one might inquire whether, in the spirited mid-air battles commonly observed, any harshness or roughness on the anterior margin of the wing might be an offensive advantage whenever actual bodily contact takes place. Again, it seems conceivable that any breaking-up of the leading edge might have some aerodynamic significance to such fast-flying birds as swallows. This, however, does not take into consideration the existing sexual dimorphism, or restriction of the modification to a few species.

Sound production. There remains only one other evident possibility: that the serrations form a mechanism for the production of some sort of sound. This appeals to me as the most likely explanation. The structures described by Sick (1937: 260, 304-306) in the two Bird of Paradise genera are said to be associated with a rustling noise made by the birds in flight, but no such function is suggested for the other comparable modifications. That spirited chases and aerial maneuvers, by groups of both sexes, play a part in the pairing and courtship of the Rough-winged Swallow, has been pointed out above. Anything that added an element of sound, particularly if it amounted to a means of sexual differentiation, could well be advantageous. It was of the greatest interest, therefore, to discover that there may indeed be a distinctive non-vocal sound produced by these swallows. I was watching a group of four or five Rough-wings, including two pairs, swooping about with unusual vigor close to an available burrow where one pair was about to begin nesting, when I first noticed a rather shrill, quickly repeated whir or whistle. (If I had heard this previously, I believe I had mistaken it for the sound of a Mourning Dove taking flight some distance away.) The Rough-wings, or at least some of them, were producing the sound, which was audible to me for only a few yards, whenever they cut the air with particularly rapid strokes. I was never sure of the sex of any individual at the critical time. On a few later occasions, I was able to hear the same distinctive sound; but it required highly favorable conditions, and I never learned anything further about its production. These observations do not prove any connection with the serrations. I was not able, in crude experiments with a compressed air jet, to produce any particular tone with a feather or a wing held in the hand. I have not heard any such whistling sound from other flying swallows, however, and consider its association with the row of projecting hooklets to be a distinct possibility. It is of special interest to speculate upon an account by Chapin (1953: 783) of the African Rough-wing *Psalidoprocne mangbettorum*, in which he says: "One bird was sometimes seen pursuing a companion with a very peculiar mode of flight, the wings moving stiffly and kept mostly below the horizontal plane of the body. This I took to be a method of courtship."

Part VI

CONCLUSIONS

Comparison of the life histories of swallows adds to the evidence, from morphological and zoogeographical studies, that the Hirundinidae are a close-knit and highly specialized, yet plastic group. The colonial and noncolonial habits are not as clearly delimited as might at first appear: nesting habits of many species vary with environmental conditions. Rather characteristic of the group seem to be the recurrent irregularities in nest-building procedures — such as protraction of the whole process, use of atypical sites (cf. Hellyar, 1927; Carpenter, 1918: 91; Monroe and Mengel, 1942; Schorger, 1920: 143), adding to the nest during laying, and sporadic building activity by adults and young (cf. Chapman, 1898; Brewster, 1898; Nice, 1935; Petersen, 1955: 260); variability in clutch size; and inconsistencies in the early stages of incubation. Swallows in all parts of the world exhibit similarly long nestling periods, and (so far as is now known) a distinctive mode of nestling development. While the patterns of breeding biology are somewhat limited by special requirements, frequent modifications of detail are to be looked for — and found — within the basic framework common to the group. Divergence and parallelism are as common in the behavior as in the morphology.

POSITION AND STATUS

Greatly improved understanding of the breeding biology of *Stelgidopteryx* calls for no essential revision of the more recent ideas of its relationships. It has a combination of behavior traits not found in any of the other swallows with which comparison is possible. Although its life history appears to have certain features in common with that of the African *Psolidoprocne* (e.g., nesting in ready-made holes, white eggs, and nonparticipation of the male in incubation), it shows many points of difference, such as much larger clutch (several species of *Psolidoprocne* lay only two eggs — cf. Chapin, 1953: 775-786), feeding of young definitely by both sexes, and much greater plasticity in choice of nesting site. In my estimation, the possession by the two genera of similar (not identical) serrations of the outer primary is no harder to explain on the basis of parallel evolution than are many other features shared by distantly related swallows; and this character may equally well be of importance in the social behavior of the birds.

The breeding biology of the Rough-wing is widely different from that of the Bank Swallow, which strongly emphasizes the probability that any morphological resemblance between the two is superficial and secondary. The Rough-wing's use of burrows only under certain conditions, its questionable digging abilities, its much less colonial habits, its preference for roosting elsewhere than in holes, and its different mode of nest construction (i.e., tendency to build more bulky nests, and the lack of a feather lining) all set it apart from the Bank. So also does the fact that the male Rough-wing takes little or no part either in nest building or in incubation.

There are many evident distinctions (e.g., in color of eggs, roles of the sexes, and number of broods per season) between the Rough-wing's breeding biology and that of the Barn and Cliff Swallows. In general social responses, migratory and prenesting behavior, means of selection of mates and nesting sites, nest building, defense of territory, and role of the male in the nesting activities, the Rough-wing has much in common with the Tree and Violet-green Swallows, and particularly with the Purple Martin, all of these latter being confined to the New World. The Rough-wing is distinguished, however, by its primary serrations, dull coloration, broad choice of nesting situations, rather simple vocal utterances, and many details of behavior on the breeding ground. Catholicity in the selection of nest sites might equally well be regarded as a primitive trait or as a high development of an adaptability common to many swallows. I am inclined to look upon the extreme diversity of habits found in the Rough-wing as involving an element of both. The plasticity in itself has become a specialization: a certain lack of order pervading the whole breeding cycle seems dependent upon varying responses to local and to temporary conditions. Even now, however, the Rough-wing almost never resorts to such cavities as boxes or holes in trees. That the bird was not fundamentally adapted to nesting in burrows is suggested by its roosting habits and by the often ample proportions of the nest itself.

Probable Neotropical origin. With the present state of our knowledge, it is impossible to trace the ancestry of *Stelgidopteryx* with any degree of certainty. Like *Progne*, *Tachycineta*, and other genera, it must have had a long history since its isolation in the New World (cf. Mayr, 1946a: 15). In view of the distribution and characters of its present-day subspecies — the juvenal plumages may represent the retention of an ancestral trait — South America seems the most probable center of origin for the Rough-wing. With regard to the northern race, the very large clutch size and the somewhat short nestling period (for a swallow) might suggest northern affinities (cf. Allen and Nice, 1952: 634); the relatively long incubation period, however, would

indicate a tropical influence (*op. cit.*: 629). To what degree these indications are significant is not yet clear. Neither has it been established how much variation has arisen within the range of the Rough-wing itself. As pointed out in the foregoing analyses, the species' present wide distribution has been of long enough duration for the evolution of distinct morphological characters, recognizable differences in notes, and some differences at least in size of clutch — quite probably there are differences in behavior not yet fully demonstrated. Whereas the marked variation in clutch size and in the start of incubation suggest imperfect ecological adjustments, they do not appear to be uncommon phenomena among northern swallows. Although it may still be extending its range gradually northward, *S. r. serripennis* can hardly be considered as a recent immigrant to North America.

Present status in North America. From most indications the Rough-wing is well adapted to life in northern latitudes. It migrates northward early in the spring, but does not start nesting activities immediately after arrival, and so may suffer less than some other swallows from inclement spring weather. The number of eggs laid is unusually large, the hatching success is good, and the percentage of survival of nestlings appears to be high. Even in large broods, young suffer little from competition for food. There is no tendency to raise a second brood, and adults and young depart for the south long before the food supply becomes precarious in the autumn. The only obvious limitation upon the bird's increase and spread is found in the availability of nesting sites, for which the species seems to be largely dependent, in most areas, upon the work of other bird species and of man.

Importance of the species. One conclusion to be drawn from my studies is that the Rough-wing's importance, or potential importance, economically, has been greatly underestimated. It is unquestionably more common in many localities than is generally realized. Its food habits, like those of all swallows, can be considered entirely beneficial. It is notable for its tolerance of disturbance, and ability to maintain itself in close proximity to civilization; in fact, the species probably derives a net benefit from man's activities. It is not known to have any undesirable behavior traits. Except for such isolated suggestions as that of Chapman (1938), who mentions the possibility of deliberately placing pipes in walled-up stream banks to encourage the "mosquito-consuming swallows," there seems to have been no published plea for special conservation efforts on behalf of this species. My work, however, has demonstrated conclusively that suitably placed nesting containers are useful for maintaining and increasing the local population. These undoubtedly could be used in a variety of

situations, in banks and walls, and about buildings and other structures as well. If properly built and placed, they would not be too much usurped by undesirable species or leave the Rough-wings abnormally exposed to predation. With provisions for cleaning the nesting chambers between seasons, such containers could be made to last for many years.

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A



B

PLATE I. Appearance of nest tubes installed: closed (A), and opened for inspection of nest contents (B).

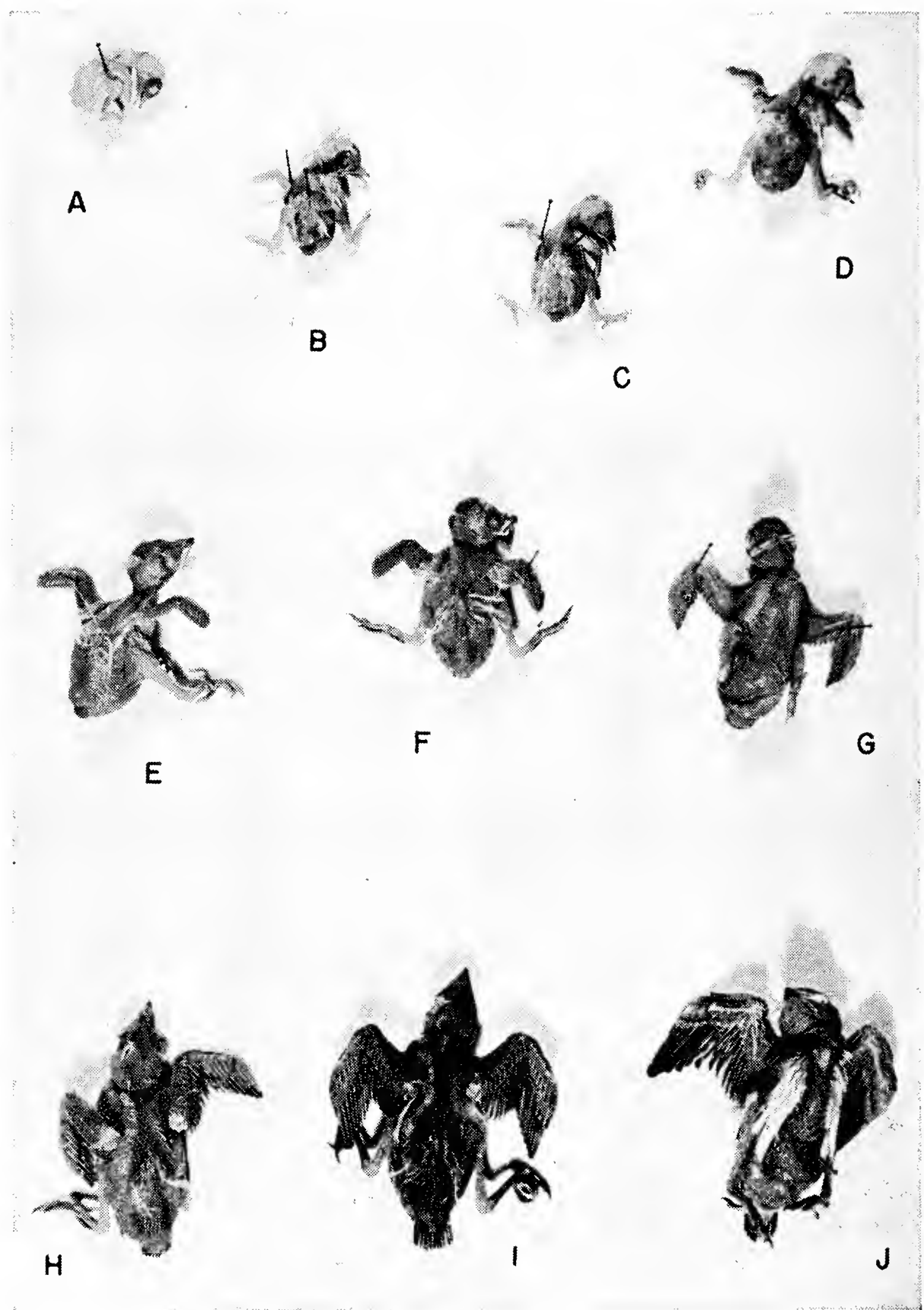


PLATE II. Rough-winged Swallow nestlings from time of hatching to nine days of age (alcoholic specimens) :

- A. Newly hatched (Nest 79, June 12, 1951; 1.2 grams).
- B. One day old (Nest 63, June 12, 1951; 2.0 grams).
- C. Two days old (Nest 76, June 12, 1951; 2.8 grams).
- D. Three days old (Nest 75, June 12, 1951; 4.3 grams).
- E. Four days old (Nest 64, June 12, 1951; 6.6 grams).
- F. Five days old (Nest 82, June 22, 1951; 7.2 grams).
- G. Six days old (Nest 65, June 20, 1951; 8.2 grams).
- H. Seven days old (Nest 77, June 20, 1951; 11.8 grams).
- I. Eight days old (Nest 108, June 21, 1952; 13.6 grams).
- J. Nine days old (Nest 63, June 20, 1951; 16.2 grams).

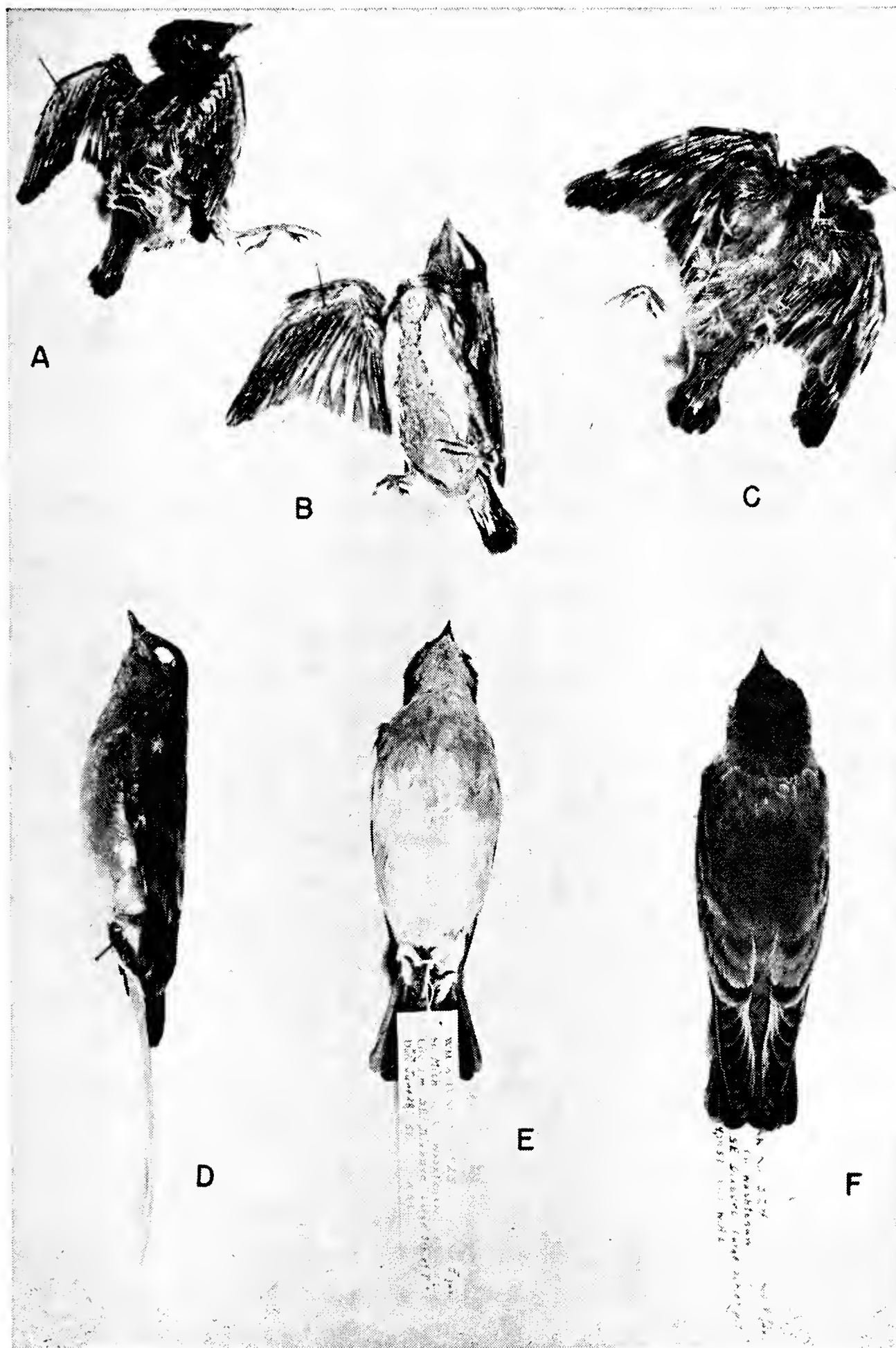


PLATE III. Rough-winged Swallow nestlings from ten days of age to nineteen days (alcoholic specimens and study skins):

- A. Ten days old (Nest 76, June 20, 1951; 15.8 grams).
- B. Eleven days old (Nest 68, June 23, 1951; 16.9 grams).
- C. Twelve days old (Nest 77, June 25, 1951; 16.7 grams).
- D. Fourteen and one-half days (Nest 12, July 11, 1949; male; 16.8 grams as found dead).
- E. Sixteen and one-half days (Nest 79, June 28, 1951; male; 16.6 grams).
- F. Nineteen days (Nest 64, June 24, 1951; 14.0 grams).

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The rough-winged swallow, Stelgidop

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